Morphology, phylogeny, and evolutionary development in the weevils (Insecta: Coleoptera: Curculionoidea)

By

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**Abstract**

Weevils (superfamily Curculionoidea) rank among the most diverse groups of extant organisms, with ~60,000 described species. They are extremely important economically, being of great agricultural significance because they associate with all major groups of plants, often with negative consequences for crops. For these reasons, weevils are also of great systematic interest: few weevil systematists remain active, and (to date) few phylogenetic studies have focused on weevils and their relatives (Curculionoidea), all utilizing few taxa (~150 taxa), leaving knowledge of weevil relationships scanty at best. In this study, the densest taxon sampling to date was implemented, consisting of 282 morphological characters scored for 577 taxa. It also represents the first study to incorporate numerous fossils into a formal cladistic analysis. In order to develop a more robust morphological character system for cladistic analysis of the higher lineages and to gain a comprehensive understanding of rostrum structure prior to developmental studies examining its formation, a comparative study also was conducted of rostrum structure throughout Curculionoidea through examination of semi-thin sections. The weevil rostrum, for example, is a key evolutionary innovation that has enabled this group to feed on and oviposit in nearly all plant tissues, giving rise to diverse life histories and tremendous diversity in rostrum form. Insights into comparative development of the rostrum will provide insight into the evolution of this key innovation that may be responsible for the explosive radiation of the lineage. Although weevils are an enormous group and countless species are significant agricultural pests, no weevil species have been utilized in developmental studies. In order to better understand the formation and evolution of this structure, transcriptomes from the developing head tissue of 4 weevil species, representing disparate clades and divergent rostral forms, and 1 outgroup (non-weevil species) were generated. While there are difficulties in

assessing differences among transcriptomes from divergent taxa, tests for differential expression patterns of transcripts were performed and a refined list of candidate genes has been produced. RNA interference experiments were performed on a subset of candidate genes to test function. This study provided insight into the developmental underpinnings that produced the profound phenotypic diversity observed in the rostrum and the genetic framework that permitted the diversification of such an immense lineage as the weevils.

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## 1. Phylogeny of Curculionoidea based on morphology


### Abstract

Weevils (superfamily Curculionoidea) rank among the most diverse groups of extant organisms, with ~60,000 described species. They are extremely important economically, being of great agricultural significance because they associate with all major groups of plants, often with negative consequences for crops. For these reasons, weevils are also of great systematic interest: few weevil systematists remain active, and (to date) few phylogenetic studies have focused on weevils and their relatives (Curculionoidea), all utilizing few taxa (~100 taxa), leaving knowledge of weevil relationships scanty at best. In this study, the densest taxon sampling to date was implemented, consisting of 282 morphological characters scored for 577 taxa. It also represents the first study to incorporate numerous fossils into a formal cladistic analysis.


### Introduction

*Weevil classification*

The first weevils, including the iconic genus *Curculio*, were described by Linnaeus (1758). Since then, nearly 60,000 species have been described and classified within the weevil superfamily Curculionoidea, a lineage estimated to possibly contain more than three times that of the currently described fauna (Oberprieler *et al.* 2007). The first classifications came by Billberg (1820) and Schönherr (1826), establishing a framework of which remnants are still visible. Crowson (1955) made vast improvements by distilling scattered concepts and establishing more cohesive groups. Subsequent classifications have worked on refining these broader concepts, as well as providing definition within specific groups (e.g., Davis 2011; Franz 2012; Kuschel 1995; Kuschel and Leschen 2003, 2011; Morimoto 1962; Morimoto and Kojima 2003; Oberprieler 2000; Oberprieler *et al.* 2007; Thompson 1992; Wanat 2001; Zherikhin & Gratshev 1995, Zimmerman 1993, 1994a, b), and much disagreement has arisen in the hierarchical positions of the various proposed groupings following the integration of cladistic methods. Most certainly due to the massive size of the weevil clade, until recently most studies have been based on fairly small and geographically restricted sample sizes, causing disparity in character references and contributing to the discordance between group concepts. Incorporation of larval data is less frequent due to the difficulties encountered in obtaining it, though despite these tribulations, moderate success has been achieved in determining its phylogenetic utility (Marvaldi and Morrone 2000; May 1993). While morphological examination has provided foundational structure to family level classification, and moderately to subfamily level, greater resolution within the Curculionidae perhaps has recently been achieved through incorporation of molecular sequence data (Haran *et al.* 2013; Marvaldi *et al.* 2002; McKenna *et al.* 2009). Although these studies certainly are of great contribution, they all suffer from limited taxon sampling and mostly have demonstrated the relative disorganization of the family and need for greater exploration of accompanying morphological data. Furthermore, with the exception of Legalov (2010a), no study has yet to incorporate fossil data in the analyses, perhaps adding extra dimensions of incongruence in time-calibrated studies. In this study, it therefore was a primary objective to incorporate a broader taxon sampling and scour the largely unexplored internal anatomy of the adult body for additional phylogenetically informative data.

*Fossil history*

In comparison to other groups of insects, in particular other beetles, the described weevil fossil record is fairly extensive, albeit with many remaining gaps. This moderate abundance is perhaps owing to their rostrum, a distinct feature often readily distinguishing them among other compression fossil material. As great disparity often arises from failed attempts to link fossil faunas to the extant lineages, it is of no surprise that weevil taxonomy also bears reminders of such incongruities in past and current classifications.

The Cenozoic and Mesozoic fossil record of weevils is quite vast. While some previous authors have provided useful reviews of parts of this history (e.g., Gratshev & Zherikhin 2003; Kuschel 1983; Legalov 2012a), each period is deserving of its own review and detailed revision. Major Mesozoic amber types and deposits and the respective researchers who have worked on them include Karatau, Kazakhstan (Arnoldi *et al.* 1977; Legalov 2009, 2010b, 2012a,b; Zherikhin 1993), Yixian Formation, China (Davis *et al.* 2013), Daohugou, China, El Montsec/Sierra del Montsec, Spain (Gratshev & Zherikhin 2000a; Soriano *et al.* 2006; Zherikhin & Gratshev 1997), Santana Formation (Crato), Brazil (Santos *et al.* 2007; Zherikhin & Gratshev 2004), and Burmese (Cognato & Grimaldi 2009; Poinar 2006; Poinar & Brown 2009), Lebanese (Kirejtshuk *et al.* 2009; Kuschel & Poinar 1993), French (Peris *et al.* in press; Soriano 2009), Spanish (Peris *et al.* in press), Baltic (Kuschel 1992; Riedel *et al.* 2012; Zherikhin 1971), and New Jersey ambers (Gratshev & Zherikhin 2000b). In particular reference to the Karatau site, hundreds of specimens have been uncovered, possibly slightly more than half of them described and representing at least several lineages of Nemonychidae, Anthribidae, and Caridae. While other families are reported in the literature from this site (e.g., Legalov 2014), these identifications are rather unclear. Although many specimens carry a certain gestalt and may indeed represent certain taxa, explicit characters are often not visible and thus unambiguous determinations unfortunately are unreliable. The Obrieniidae, for instance, is one lineage with a weevil-like gestalt, and as such, it occasionally has been included within Curculionoidea (Legalov 2012b; Zherikhin & Gratshev 1993); however, the structure of at least the sternum and elytral striae appear to indicate either a derived lineage of Archostemata or basal lineage of Polyphaga. Some rather magnificent anthribids have recently come from Karatau (Legalov 2011), including an interesting incorporation of the previously described Protoscelinae into Anthribidae (Legalov 2013). Upon closer inspection, the similarities of the Protoscelinae to some extant lineages of Anthribidae (Anthribinae: Ptychoderini) is rather striking, including a loose antennal club, sub-basal carinae on the pronotum, faint elytral striae, separate labrum, and medio-longitudinal groove on the 7$^{th}$ abdominal tergite. The cerambycid-like appearance of these groups, after accounting for their apparent old age, may indicate a fairly basal position of this group in the Anthribidae and entire Curculionoidea.

Although relatively less work has been accomplished on the Cenozoic fauna, particularly recently, there are several amber types and deposits containing much undescribed material, including the Green River and Kishenehn Formations, Colorado, USA, Eckfeld Maar, Germany, the Skarðsströnd–Mókollsdalur and Hreðavatn–Stafholt Formations, Iceland, and Dominican amber. These faunas perhaps receive less attention due to their somewhat smaller impact on phylogeny, difficulty in identification (as many taxa are members of the largest radiation, Curculionidae), and immense volume of material.

## Materials and methods

### *Taxon sampling*

Extant taxa: Taxon sampling was directed utilizing Alonso-Zarazaga and Lyal (1999), Oberprieler *et al.* (2007), Zherikhin and Gratshev (1995), and Thompson (1992) in order to reduce any *a priori* bias, though the classification for taxon sampling follows that of Alonso-Zarazaga and Lyal (1999). The final analysis included a total of 577 taxa (see Appendix B for character matrix). Exemplars from nearly all extant subfamilies within Curculionoidea were sampled, with the exception of a few in Oxycorynidae (Oxycoryninae, Afrocoryninae, Hispodinae, Metrioxeninae), Attelabidae (Archolabinae), Brentidae (Pholidochlamydinae), Apionidae (Myrmacicelinae, Rhinorhynchidiinae), Raymondionymidae (Myrtonyminae), and Curculionidae (Xiphaspidinae). Outgroup taxa were few but considered adequate for rooting of the tree, using one species from Cucujidae, one from Orsodacnidae, and one from Chrysomelidae.

Fossil taxa: Taxon sampling of fossil taxa focused heavily on Mesozoic taxa, a large proportion of which were from Karatau. All known material from the Yixian Formation was included, as well as an undescribed specimen from Daohugou, and several specimens from Mesozoic ambers were included. In total, 173 fossil specimens were coded for morphological characters and included in subsequent analyses.

Taxa were examined at and borrowed from the following institutions:

USNM – National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, D.C., USA.

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

CMNC – Canadian Museum of Nature, Ottawa, Canada.

CNC - Canadian National Collection, Ottawa, Canada.

IOZ CAS – Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

CNU - Capital Normal University, Beijing, China.

CAS – California Academy of Sciences, San Francisco, California, USA.

FMNH – Field Museum of Natural History, Chicago, Illinois, USA.

ELKU - Entomological Laboratory, Kyushu University, Fukuoka, Japan.

NIAES - National Institute of Agro-Environmental Sciences, Tsukuba, Japan.

TUA - Tokyo University of Agriculture, Atsugi, Japan.

ANIC - Australian National Insect Collection, CSIRO, Canberra, Australia.

NZAC - New Zealand Arthropod Collection, Auckland, New Zealand.

PI RAS - Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia.

*Specimen dissection and preparation*

Body and genitalia dissection:

All dissections were performed using an Olympus SZ60 microscope. For each taxon in which multiple specimens were available, a full-body dissection was done for the male and abdominal dissection for the female (including genitalia). In some taxa, full-body dissections were not permited by the borrowing institution and thus only abdominal dissections were done for those males.

For body dissections, specimens were first relaxed by soaking them in warm water for ~10-15 minutes, the duration depending on the size of the specimen. The head, pro-thorax, meso-meta-thorax complex, and abdomen were then separated. Before digesting any internal tissues, the elytra and hind wings were removed and stored in glycerin, as digesting was not required for these parts. The remaining dissected parts were digested in a weak (~10%) KOH solution for 10-15 minutes, again depending on the size of the specimen. Following digestion, all remaining internal tissues were removed and the sclerotized parts cleaned. The meso- and meta-nota were separated from the mesepimera, metepisterna, and metepimera, and subsequently separated from each other. The terga were separated from the sterna along one side, and the genitalia removed together with the $8^{th}$ tergum. After dissections were completed, all parts were stored in glycerin.

Mouthpart dissection:

Following dissection of the body, the head was digested further in 10% KOH for ~15-30 minutes, depending on specimen size. Under the microscope, the head was placed with the ventral side facing upwards. One pair of fine-tipped forceps was used to stabilize the rostrum while another pair was used to gently separate the postmentum of the labium from the submentum of the rostrum. The maxillae were subsequently removed in a similar fashion, separating them from the submentum at the cardo-submentum junction. The mandibles were then removed, separating them from the postcoila.

Hind wing and mouthpart preparation:

Following dissection of the hind wing from the thorax and mouthparts from the rostrum, these parts were then mounted on glass microscope slides for further examination. One hind wing from each body dissection, the labium, maxilla, and mandibles from the same specimen were mounted on a slide in Euparal mounting medium. The slide was then placed on a slide warmer to dry the mounting mediums.

Scanning Electron Microscopy:

All SEM images were captured using a LEO 1550 FESEM. Specimens were mounted on an SEM stub using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite. Whole specimens were placed on insect pins or glued to paper points, securing the pin or point on an SEM stub using Leit-C-Plast. Dissected parts were mounted on a stub by securing them with a thin layer of colloidal graphite. After the desired parts were mounted, coating was performed using gold.

*Character Discussion*

A total of 282 morphological characters were coded from a diverse selection of adult sclerotized structures throughout the body. Appendix A provides this list of characters and brief descriptions and explanations for clarity of character delimitations and their respective states. While much of the specific character explanations are provided within this appendix, the more general aspects of these morphological features are described below, including some features which may be of some phylogenetic significance but were not coded in this study.

Mouthpart morphology follows Morimoto (1962), Morimoto *et al.* (2006), and Ting (1936). Nearly 40 characters were extracted from the labium, maxillae, and mandibles (Figs. 1-3). Although the mouthparts have been studied by several authors and their diversity throughout the superfamily fairly well documented (Calder 1989; Dennell 1942; Morimoto 1962; Ting 1936), one oral structure which has gone unnoticed is the pharyngeal plate. This structure is visible in semi-thin sections as a broadly curved, sclerotized support immediately below the pharynx and present only near the rostrum apex. After removing the mouthparts from the oral cavity, being careful not to separate them to their basal connections, the pharyngeal plate is revealed to be a fairly large sclerotized area with anterior arms which support the basal articulation of the maxillae (Figs. 4-22).

The mesonotum (Fig. 23) and metanotum (Figs. 24-25) are fairly unexplored areas of adult morphology, both yielding many characters and apparently quite informative at the family level and at the subfamily level within at least Curculionidae. Wood (1986), in his attempts to place Scolytidae and Platypodidae, was the only weevil researcher who gave attention to these areas.

The hind wing venation (Fig. 26) has been studied rather extensively, largely due to the thorough work of Zherikhin and Gratshev (1995). This grand study examined the venation of multiple exemplars in nearly every subfamily throughout the superfamily, extracting much phylogenetic information (though not analyzing it in a cladistic framework) and providing a seminal reference for this morphological structure. The axillary sclerites (Figs. 27-62), however, have not received such decisive attention, perhaps due to difficulty in their examination and the relatively smaller amount of characters information they provide. The most detailed account was provided by Shurtleff (1961) in his study of axillary sclerites in Coleoptera. While this area of this hind wing is relatively stable with regards to morphological change, a few characters were extracted which are indicative of higher-level relationships.

*Phylogenetic methods*

Two different matrices were analyzed in order to search for and identify possible topological effects of included taxa containing greater than 60% missing data, namely the compression fossil taxa. Such matrices were the full matrix and reduced taxon matrix (RTM). Character matrices were constructed in Mesquite (Maddison and Maddison 2011) and phylogenetic analyses were performed using Tree analysis using New Technology (TNT; Goloboff *et al.* 2003). Runs in TNT consisted of implementing sectorial searches (SS) with tree drifting (TD) and tree fusing (TF) and ratchet runs with TD and TF. The final strict consensus trees (for both full and RTM) was computed using TNT by implementing 600 random addition sequences, and 800 ratchet iterations, including 100 cycles of both TD and TF per iteration.

## Results

### *Phylogeny*

Analysis of the full dataset resulted in 108 most-parsimonious trees of L=7468, Ci=6, Ri=80. The strict consensus tree resulting from analysis of the full morphological dataset (including all fossil taxa) is presented in figures 63, 64, 65-68, yielding a tree of L=8221, Ci=6, Ri=77. A 50% majority rules tree was also computed for the full dataset and had L=7546, Ci=6, Ri=79. Analysis of the RTM (excluding most compression fossil taxa) resulted in 178 most-parsimonious trees of L=7356, Ci=6, Ri=77. The strict consensus tree resulting from the analysis of the RTM is presented in figures 69-73, yielding a tree of L=7726, Ci=6, Ri=76. A 50% majority rules tree was also computed for the RTM (Figs. 74-82) and had L=7395, Ci=6, Ri=77. Results from both analyses illustrate the following relationships: a monophyletic Nemonychidae sister to both Belidae and Anthribidae; Belidae appears paraphyletic with Nemonychidae and the Oxycoryninae appear at the base of Anthribidae; Attelabidae is monophyletic, with sister groups Attelabinae and Rhynchitinae; Caridae appears monophyletic, though with the taxa comprising the nebulous fossil group Abrocarina as sister; Ithyceridae is basal to the series of monophyletic subfamilies included in Brentidae, the first being Brentinae, followed by a clade of reciprocally monophyletic Nanophyinae and Apioninae; a monophyletic Brachyceridae comes next, then combined clade of Raymondionymidae and Cryptolaryngidae; Erirhinidae is polyphyletic before the clade containing a monophyletic Bagoinae and Scolytidae + Platypodidae + Dryophthoridae; the subsequent clade contains Curculioninae sister to Cossoninae and Entiminae, all monophyletic groups excepting parts of Entiminae (which contain taxa adjacent to Cyclominae); the next grouping contains a paraphyletic Cyclominae with respect to some parts of Entiminae and Hyperinae, these groups basal to a combined clade of Molytinae + Lixinae + Mesoptilinae; proceeding further comes an apparently monophyletic Cryptorhynchinae followed by a polyphyletic Conoderinae which sits at the base of a clade containing the monophyletic Baridinae and Ceutorhynchinae as sister groups.

## Discussion

### *Congruence with past phylogenetic studies*

While the general topology including several of the basal families is fairly consistent with previous studies (e.g., Haran *et al.* 2013; Marvaldi *et al.* 2002; McKenna *et al.* 2009), the higher Curculionidae *s.l.*, beginning around Brachyceridae, is rather dissimilar. This incongruence appears to be more of an artifact of taxon sampling, as several of the taxa within Curculionidae, which undoubtedly belong to the same clades and should group together, are separated in disparate clades. As with any phylogenetic study, a broad sampling is integral towards the goal of attempting to accurately determine evolutionary history, sampling which includes a range of primitive and derived lineages with respect to their branching patterns. Such a statement is of even greater importance when considering very old clades or those which have great diversity and size, such as Curculionoidea. While the study herein may also contain areas of topological error, the resulting relationships at least appear to be more consistent due to the much larger and more diverse taxon sampling.

*Implications towards weevil classification*

As a result of including many fossil taxa, including several amber taxa from which a comparatively greater number of characters could be extracted, the topology of the basal curculionoid families appears fairly stable with the exception of Nemonychidae, Anthribidae, and Belidae. While it is apparent that these lineages are most basal within the superfamily, the topology at this basal area does not seem as clear as previous studies have concluded. This slight lack of clarity is mostly due to re-examination of described and some undescribed fossil material. Although the topology of the higher Curculionidae appears problematic, this study shows a much improved hypothesis for delineation of the several curculionid subfamilies and their relationships. Many of the previously proposed clades show some amount of paraphyletic and polyphyletic groups, and in these cases their delineation needs to be redefined. In a few cases where pectinations are observed at the base of the clades, such as in Conoderinae, it is possible that these areas may see little improvement in terms of improved topological resolution, as they often represent graded transition zones in the evolution of larger, more homogeneous clades (Davis 2011).

The position of Scolytidae and Platypodidae as sister to Dryophthoridae is somewhat different to previous studies, in which Scolytidae has been placed more deeply nested within Curculionidae. Although several molecular studies have determined placement of Scolytidae and Platypodidae in Curculionidae, the resulting relationships are not entirely consistent. Despite the results presented herein, this result is still considered somewhat contentious due to a comparatively long branch on the Scolytidae + Platypodidae clade and the inability to more completely sample the more primitive taxa within these clades. While long branches with morphological data may be entirely indicative of increased evolutionary rates and selective pressures over relatively short periods of time; however, these topologies may also have been reconstructed incorrectly due to gaps in taxon sampling, which had they been sampled, would demonstrate branches of more moderate length. Such may be the case with the two aforementioned clades. While most of the scolytine and platypodine taxa demonstrate highly apomorphic morphology, including the two oldest known fossil taxa from the Mesozoic, a few taxa appear to retain plesiomorphic features which are familiar to the Nemonychidae and Anthribidae. A more robust conclusion perhaps only will be attained through further sampling of a few additional primitive taxa.

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## Figure legends

**Figs. 1-3**. Mouthparts of *Piesocorynus sellatus* (Anthribidae). 1, labium; 2, maxilla; 3, mandible.

**Figs. 4-8**. Dissections and illustrations showing pharyngeal plate. 4-5, photomicrographs (Cyclominae). 4, dorsal aspect; 5, ventral aspect. 6-8, *Tanyrhynchus* sp. (Entiminae). 6, photomicrograph, ventral aspect; 7, illustration, ventral aspect; 8, illustration, lateral aspect.

**Figs. 9-12**. Illustrations showing pharyngeal plate, *Aegorhinus nodipennis* (Cyclominae). 9-10, ventral aspect; 11-12, lateral aspect.

**Figs. 13-17**. Illustrations showing pharyngeal plate, *Premnotrypes vorax* (Entiminae). 13-16, ventral aspect; 17, lateral aspect.

**Figs. 18-22**. Dissections and illustrations showing pharyngeal plate. 18-19, *Brachyderes lusitanicus* (Entiminae). 18, ventral aspect; 19, lateral aspect. 20-22, photomicrographs, ventral aspects. 20, *Phrissotrichum tubiferum* (Apionidae); 21, *Heilipodus polygluttatus* (Molytinae); 22, *Gerstaeckeria lecontei* (Cryptorhynchinae).

**Figs. 23-25**. Thoracic structures, *Mecomacer scambus* (Nemonychidae). 23, photomicrograph of mesonotum, dorsal aspect; 24, photomicrograph of metanotum, dorsal aspect; 25, illustration of metanotum.

**Figs. 26-27**. Hind wing. 26, illustration of hind wing and general venation in Curculionoidea. 27, photomicrograph of base of hind wing, showing axillary sclerites, *Cerambyrhynchus schoenherri* (Anthribidae).

**Figs. 28-33**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Cucujus clavipes* (Cucujidae); 2, *Orsodacne atra childreni* (Orsodacnidae); 3, *Fidia viticida* (Chrysomelidae); 4, *Cimberis* sp. (Curculionoidea: Nemonychidae); 5, *Cerambyrhynchus schoenherri* (Anthribidae); 6, *Corrhecerus* sp. (Anthribidae).

**Figs. 34-39**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Ptychoderes sp.* (Anthribidae); 2, *Rhinotia sp.* (Belidae); 3, *Dicordylus marmoratus* (Belidae); 4, *Parallocorynus bicolor* (Belidae); 5, *Attelabus nigripes* (Attelabidae); 6, *Haplorhynchites aeneus* (Attelabidae).

**Figs. 40-45**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Car sp.* (Caridae); 2, *Brentus anchorago* (Brentidae); 3, *Noterapion meorrhynchum* (Brentidae); 4, *Dieckmanniellus nitidulus* (Brentidae); 5, *Nanophyes marmoratus* (Brentidae); 6, *Aporhina* sp. (Eurhynchidae).

**Figs. 46-51**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Ithycerus novemboracensis* (Ithyceridae); 2, *Desmidophorus sp.* (Brachyceridae); 3, *Notaris (Erirrhinus) festuca* (Erirhinidae); 4, *Sphenophorus parvulus* (Dryophthoridae); 5, *Scolytus multistriatus* (Scolytidae); 6, *Phloeoborus punctatorufosus* (Scolytidae).

**Figs. 52-57**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Hylastes parallelus* (Scolytidae); 2, *Schedlarius mexicanus* (Platypodidae); 3, *Tesserocerus inermis* (Platypodidae); 4, *Homalinotus dorsalis* (Curculionidae: Molytinae); 5, *Rhinochenus stigma* (Cryptorhynchinae); 6, *Tyloderma foveolatum* (Cryptorhynchinae).

**Figs. 58-62**. Photomicrographs of base of hind wing, showing axillary sclerites. 1, *Tanymecus confusus* (Entiminae); 2, *Anthonomus fulvus* (Curculioninae); 3, *Zygops temporarius* (Conoderinae); 4, *Araucarius sp.* (Cossoninae); 5, *Hydronomus sinuatocollis* (Bagoinae).

**Fig. 63**. Strict consensus tree of 108 trees resulting from analysis of full dataset, L=8221, Ci=6, Ri=77. Family-level clades of Curculionoidea are labeled.

**Fig. 64**. Strict consensus tree of 108 trees resulting from analysis of full dataset, L=8221, Ci=6, Ri=77. Clades within Curculionidae are labeled.

**Fig. 65**. Strict consensus tree of 108 trees resulting from analysis of full dataset (part 1), L=8221, Ci=6, Ri=77.

**Fig. 66**. Strict consensus tree of 108 trees resulting from analysis of full dataset (part 2), L=8221, Ci=6, Ri=77.

**Fig. 67**. Strict consensus tree of 108 trees resulting from analysis of full dataset (part 3), L=8221, Ci=6, Ri=77.

**Fig. 68**. Strict consensus tree of 108 trees resulting from analysis of full dataset (part 4), L=8221, Ci=6, Ri=77.

**Fig. 69**. Strict consensus tree of 178 trees resulting from analysis of RTM (part 1), L=7726, Ci=6, Ri=76.

**Fig. 70**. Strict consensus tree of 178 trees resulting from analysis of RTM (part 2), L=7726, Ci=6, Ri=76.

**Fig. 71**. Strict consensus tree of 178 trees resulting from analysis of RTM (part 3), L=7726, Ci=6, Ri=76.

**Fig. 72**. Strict consensus tree of 178 trees resulting from analysis of RTM (part 4), L=7726, Ci=6, Ri=76.

**Fig. 73**. Strict consensus tree of 178 trees resulting from analysis of RTM (part 5), L=7726, Ci=6, Ri=76.

**Fig. 74**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 1), L=7395, Ci=6, Ri=77.

**Fig. 75**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 2), L=7395, Ci=6, Ri=77.

**Fig. 76**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 3), L=7395, Ci=6, Ri=77.

**Fig. 77**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 4), L=7395, Ci=6, Ri=77.

**Fig. 78**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 5), L=7395, Ci=6, Ri=77.

**Fig. 79**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 6), L=7395, Ci=6, Ri=77.

**Fig. 80**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 7), L=7395, Ci=6, Ri=77.

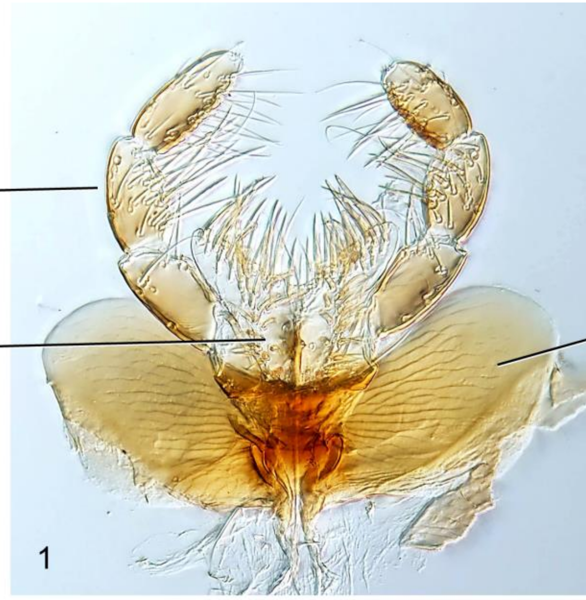
**Fig. 81**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 8), L=7395, Ci=6, Ri=77.

**Fig. 82**. 50% majority rules tree of 178 trees resulting from analysis of RTM (part 9), L=7395, Ci=6, Ri=77.

**Appendices**

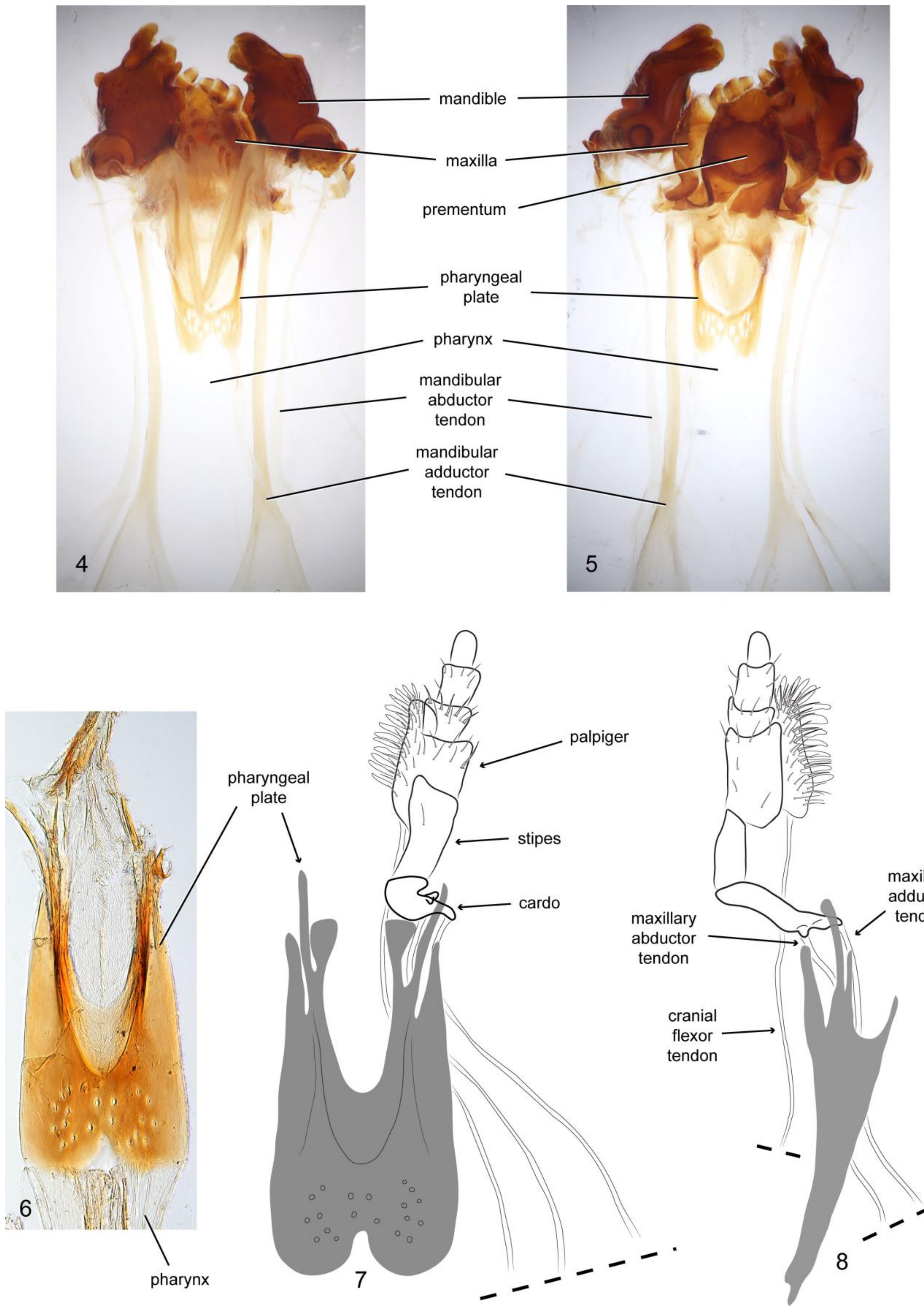
**Appendix A**. A list showing the 282 morphological characters and states encoded in this study.

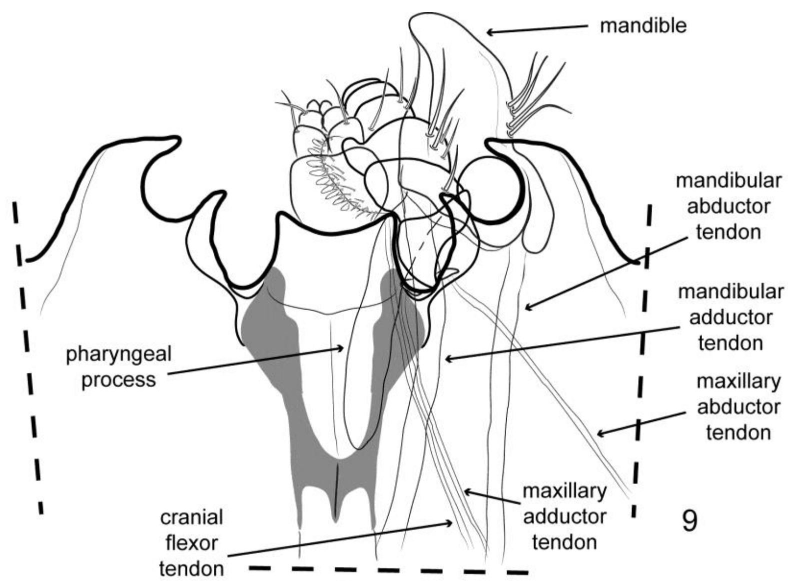
**Appendix B**. Character matrix containing 282 morphological characters scored for 577 taxa.


labial
palpus
prementum
postmentum
1


maxillary
palpus
palpiger
stipes
cardo
galea
lacinia
2

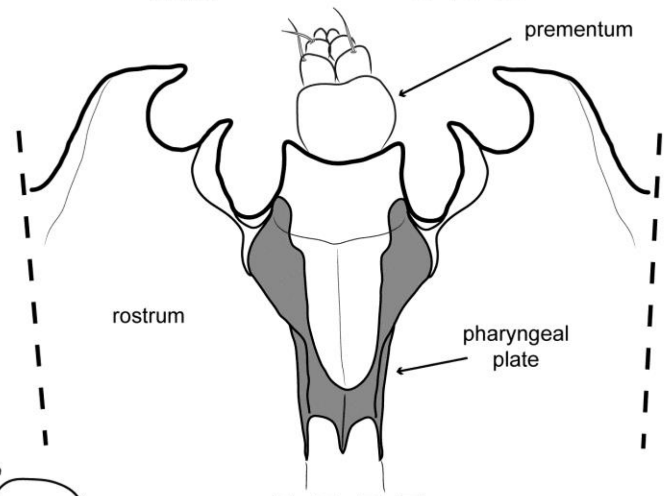

incisor
teeth
molar
region
adductor
tendon
abductor
tendon
3


mandible
maxilla
prementum
pharyngeal plate
pharynx
mandibular abductor tendon
mandibular adductor tendon
4
5
pharyngeal plate
pharynx
6
palpiger
stipes
cardo
7
maxillary adductor tendon
maxillary abductor tendon
cranial flexor tendon
8



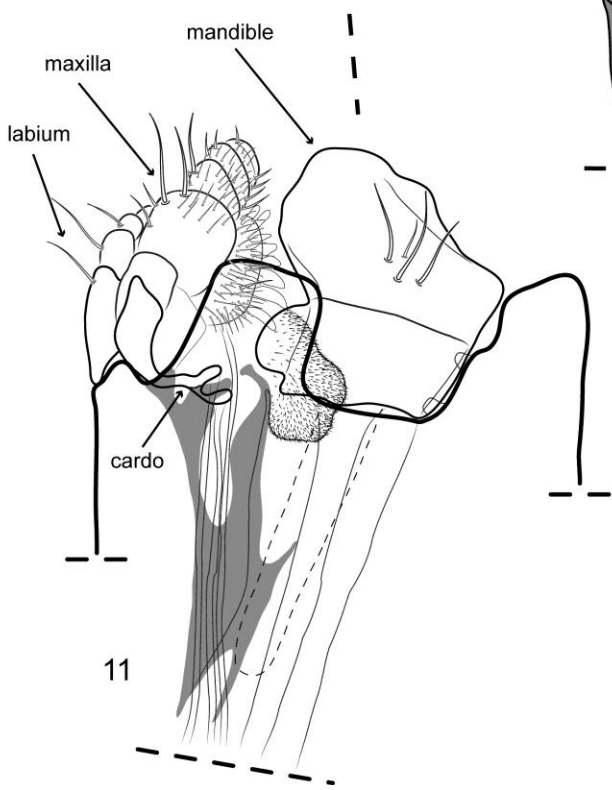
mandible
mandibular abductor tendon
mandibular adductor tendon
maxillary abductor tendon
pharyngeal process
maxillary adductor tendon
cranial flexor tendon


9



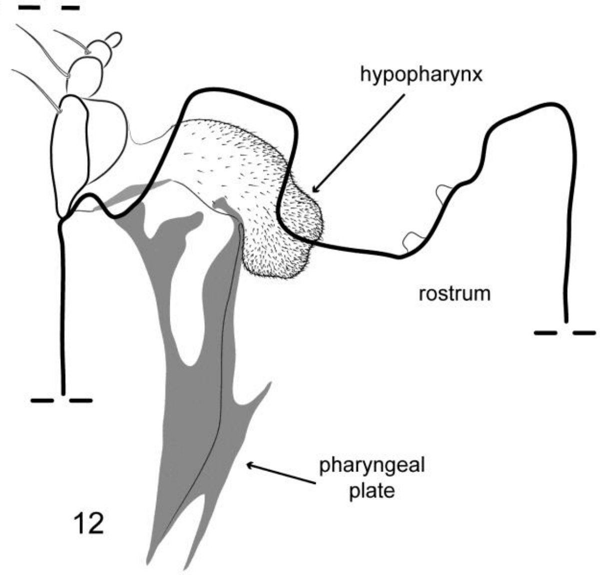
prementum
rostrum
pharyngeal plate


10



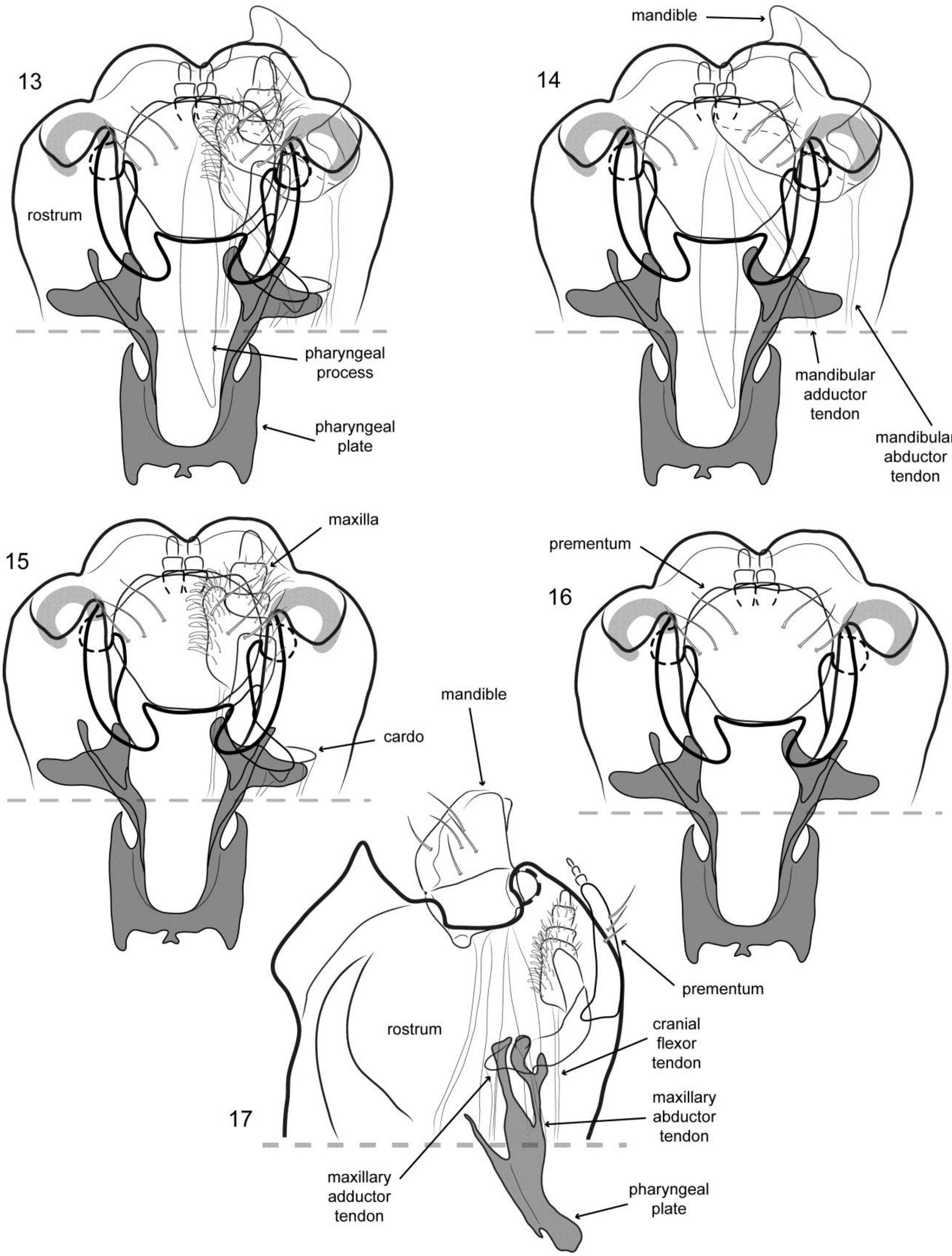
mandible
maxilla
labium
cardo


11

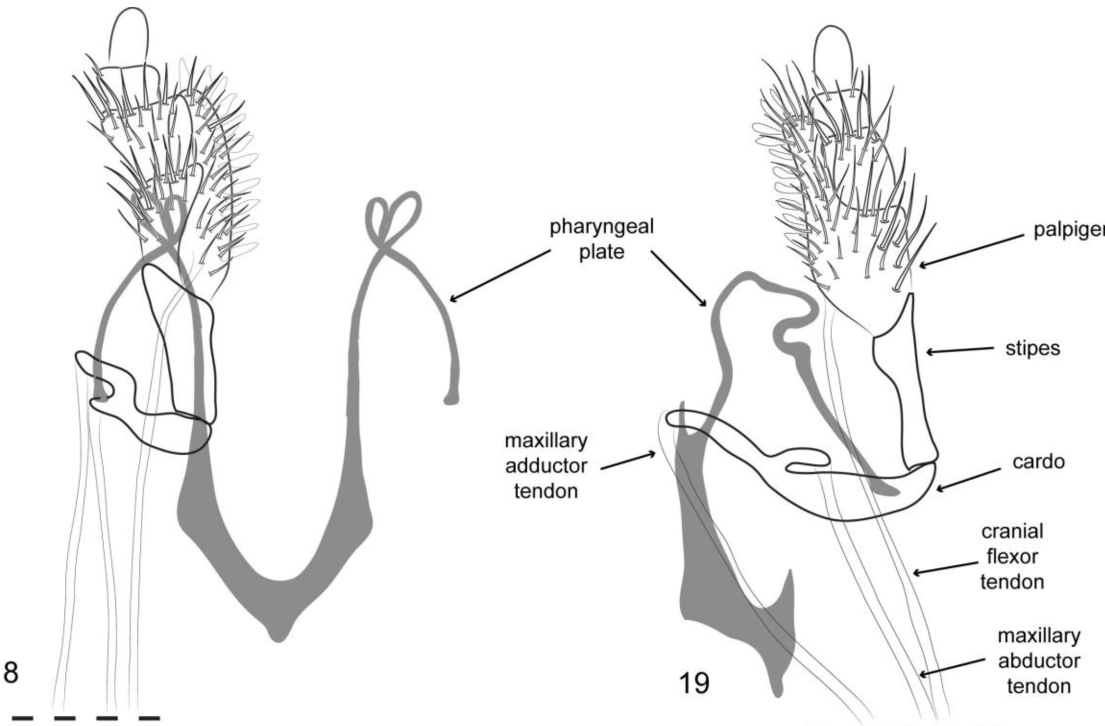


hypopharynx
rostrum
pharyngeal plate

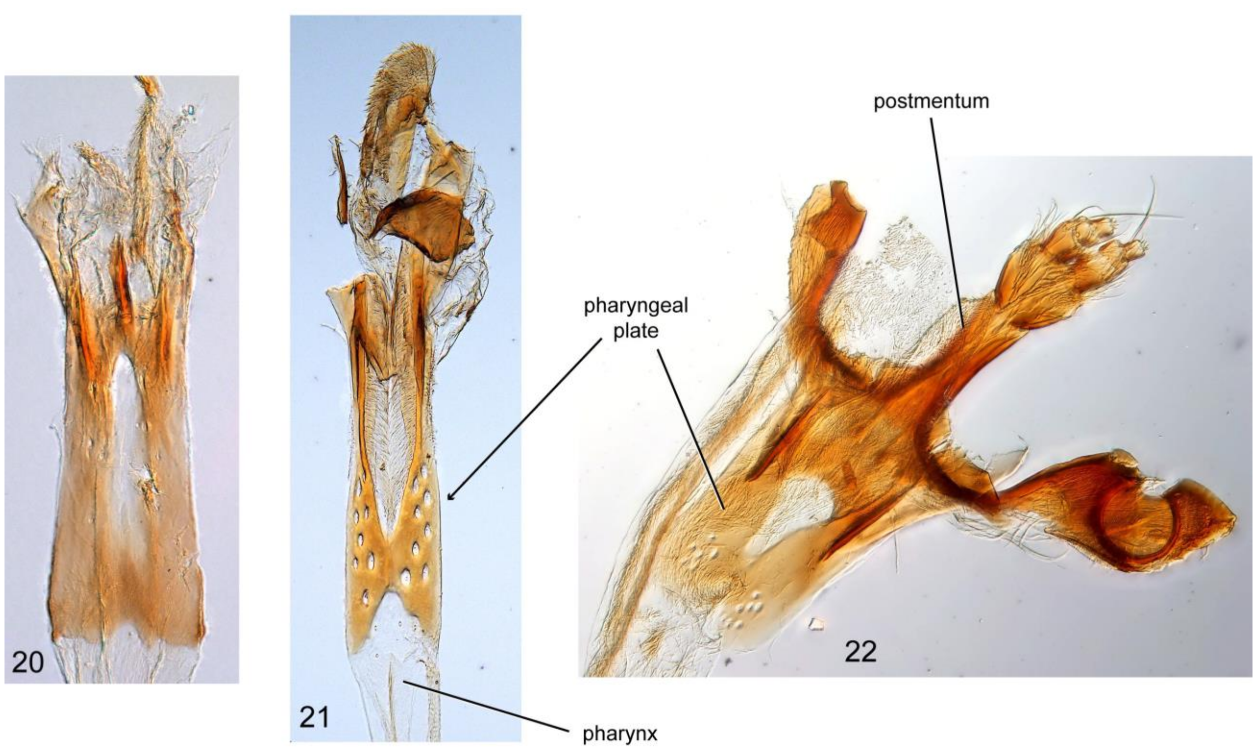

12



13
rostrum
pharyngeal process
pharyngeal plate
14
mandible
mandibular adductor tendon
mandibular abductor tendon
15
maxilla
cardo
16
prementum
17
mandible
prementum
rostrum
cranial flexor tendon
maxillary abductor tendon
maxillary adductor tendon
pharyngeal plate



pharyngeal plate
palpiger
stipes
maxillary adductor tendon
cardo
cranial flexor tendon
maxillary abductor tendon
18
19

postmentum
pharyngeal plate
pharyngeal plate
pharynx
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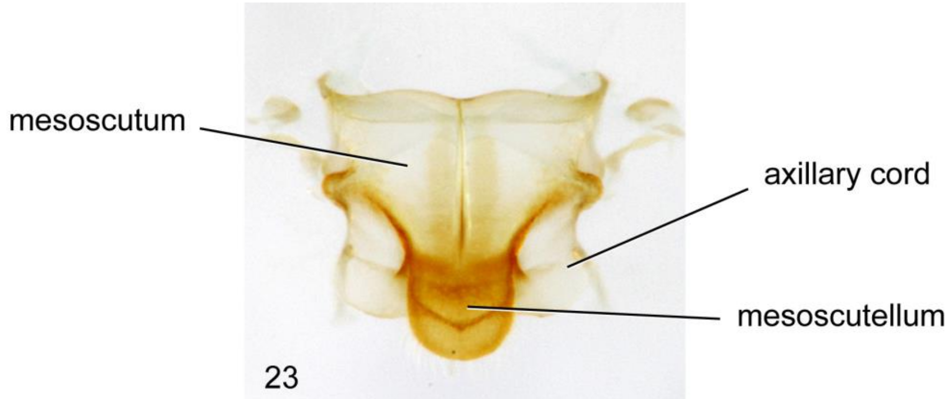
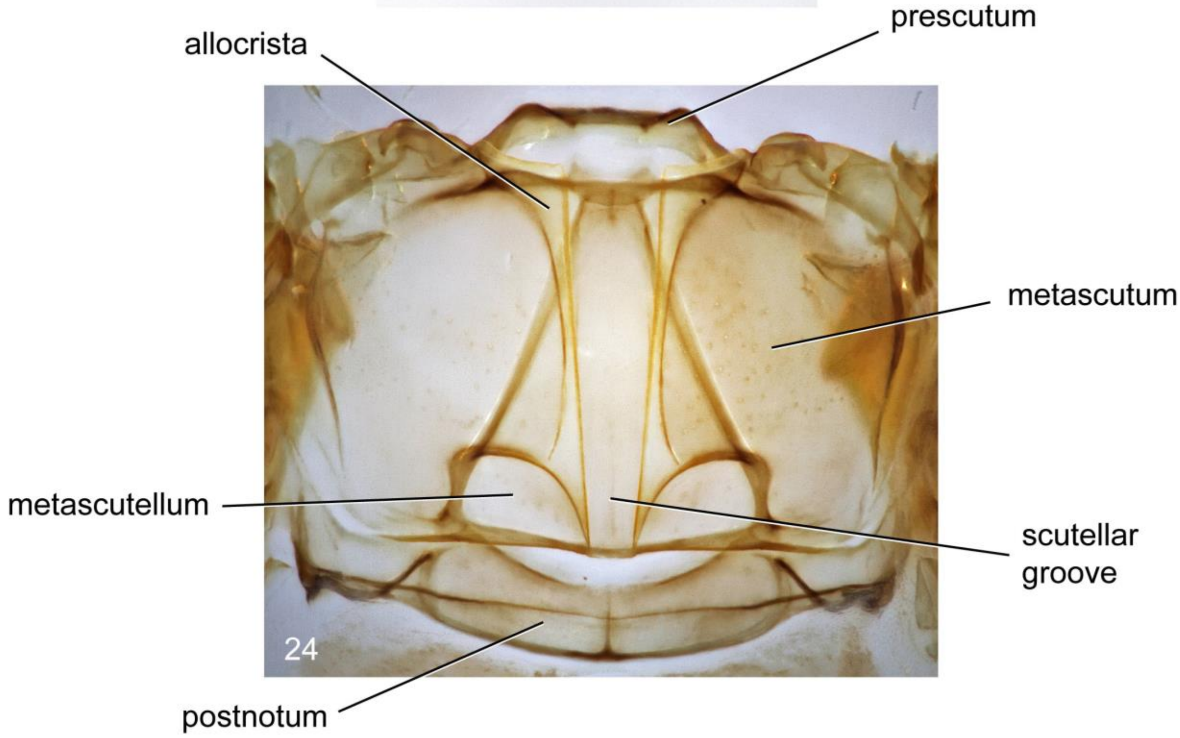
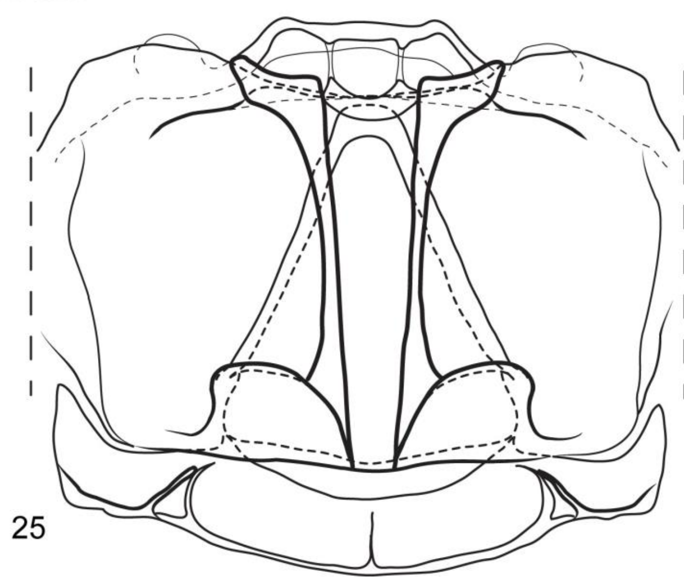
21
22


mesoscutum
axillary cord
mesoscutellum
23


allocrista
prescutum
metascutum
metascutellum
scutellar groove
24
postnotum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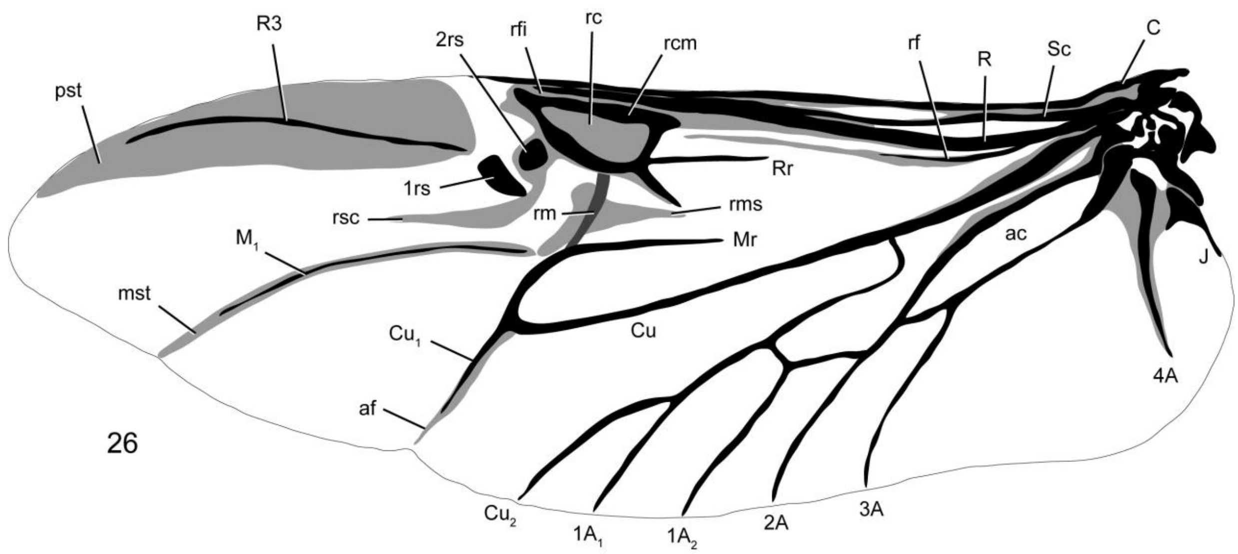
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2rs
rfi
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rcm
rf
R
Sc
C
1rs
Rr
rsc
rm
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M1
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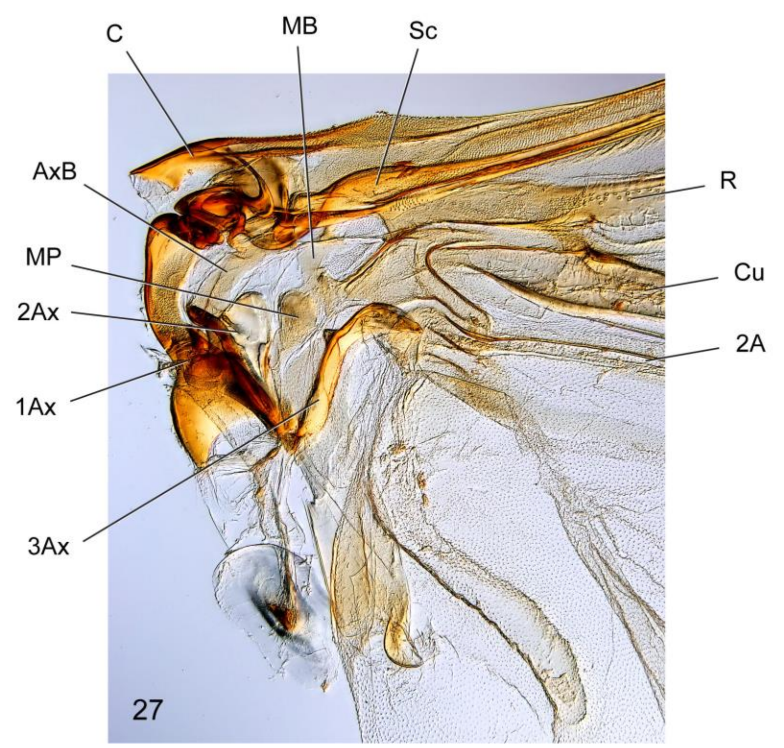
J
mst
Cu1
Cu
af
4A
Cu2
1A1
1A2
2A
3A

26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Sc
AxB
R
MP
Cu
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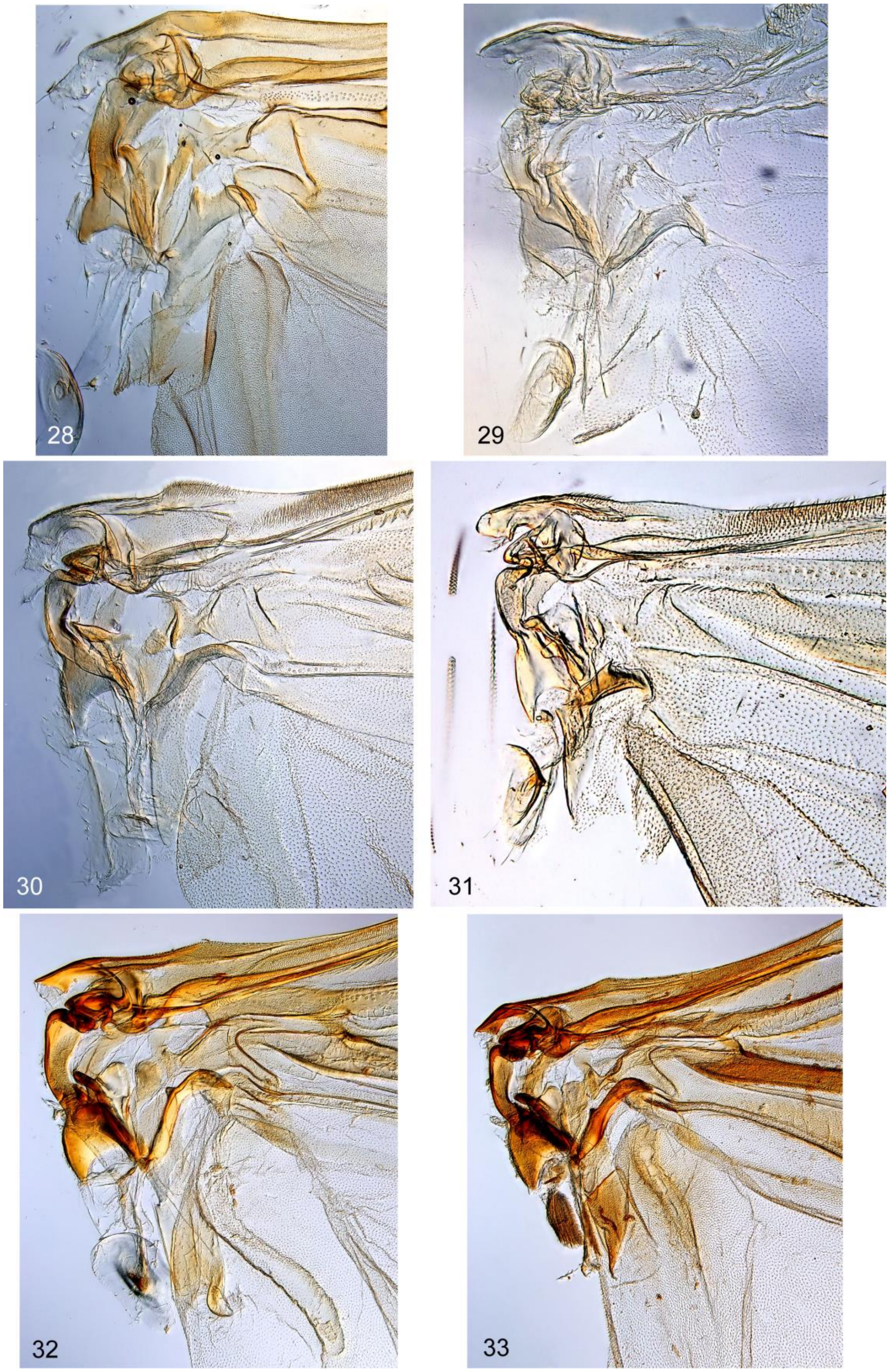
2A
1Ax
3Ax

27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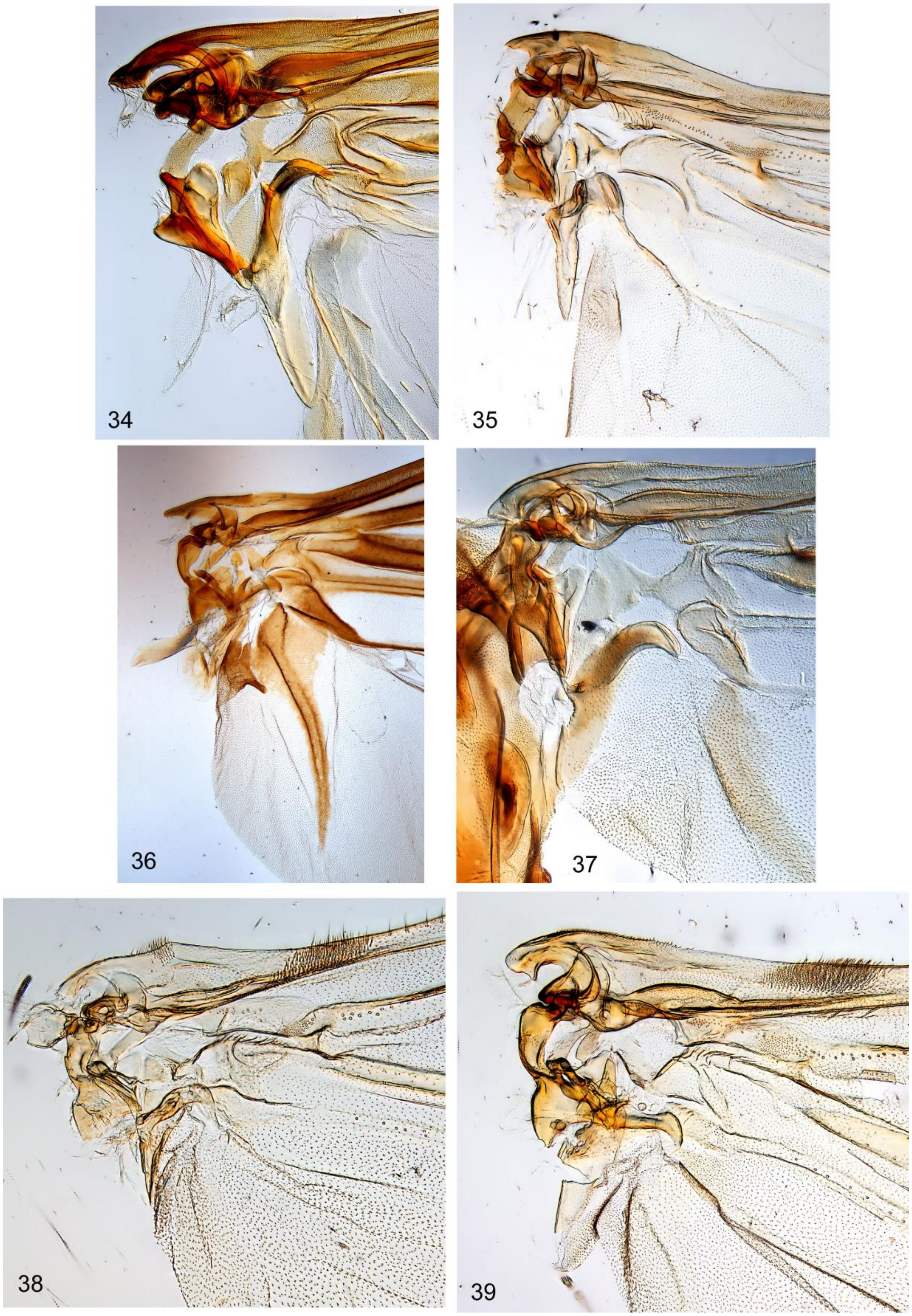
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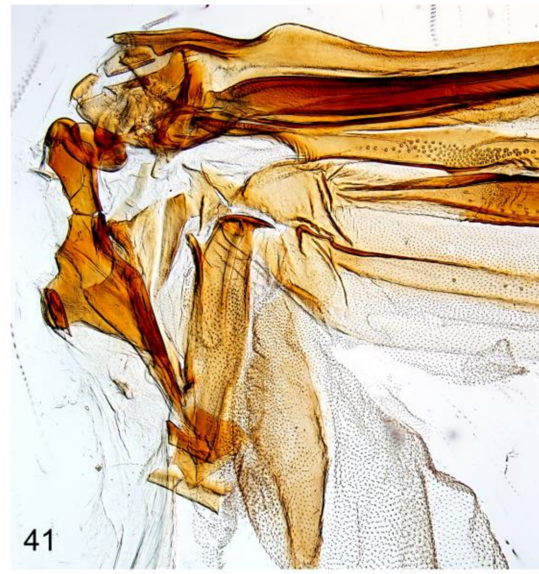
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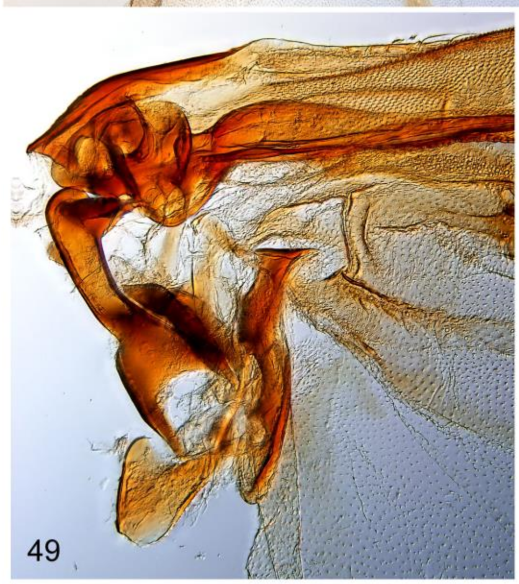
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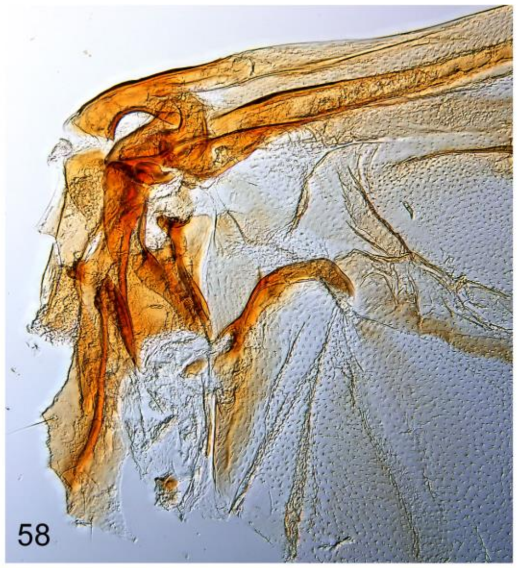
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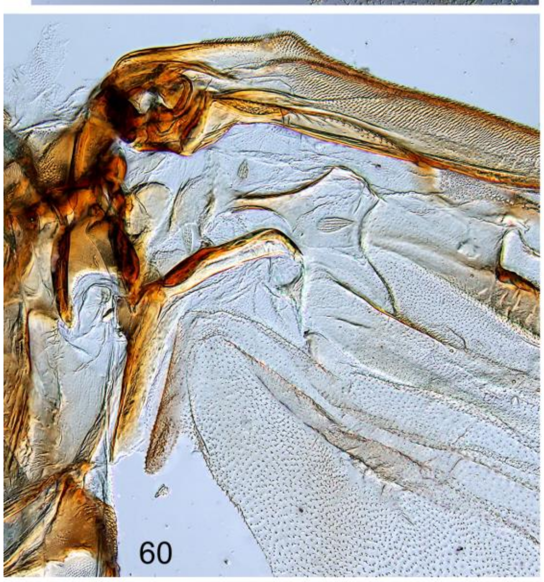
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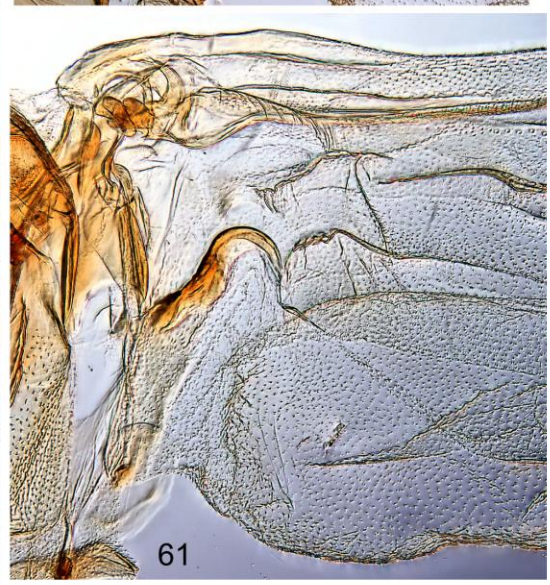
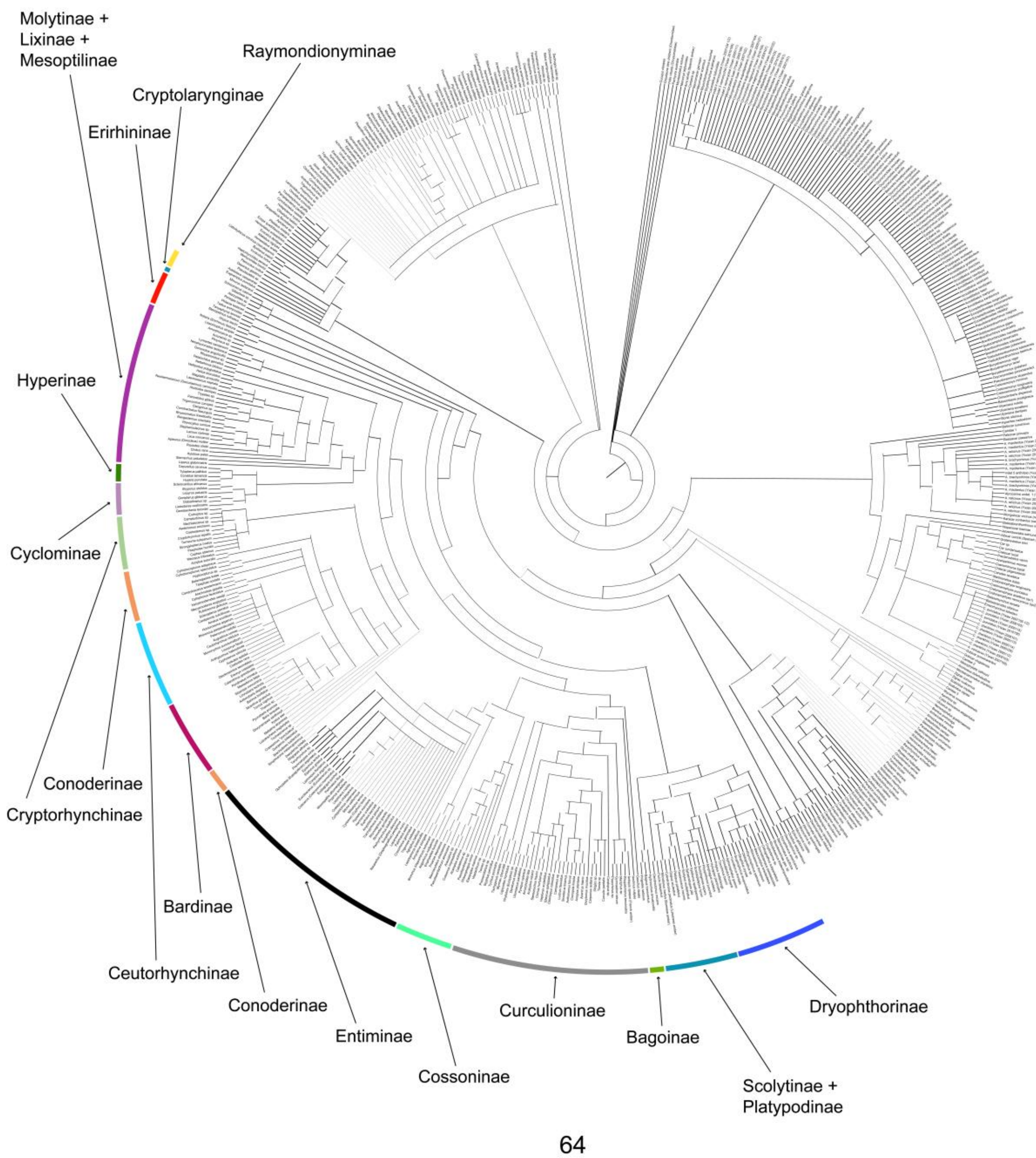
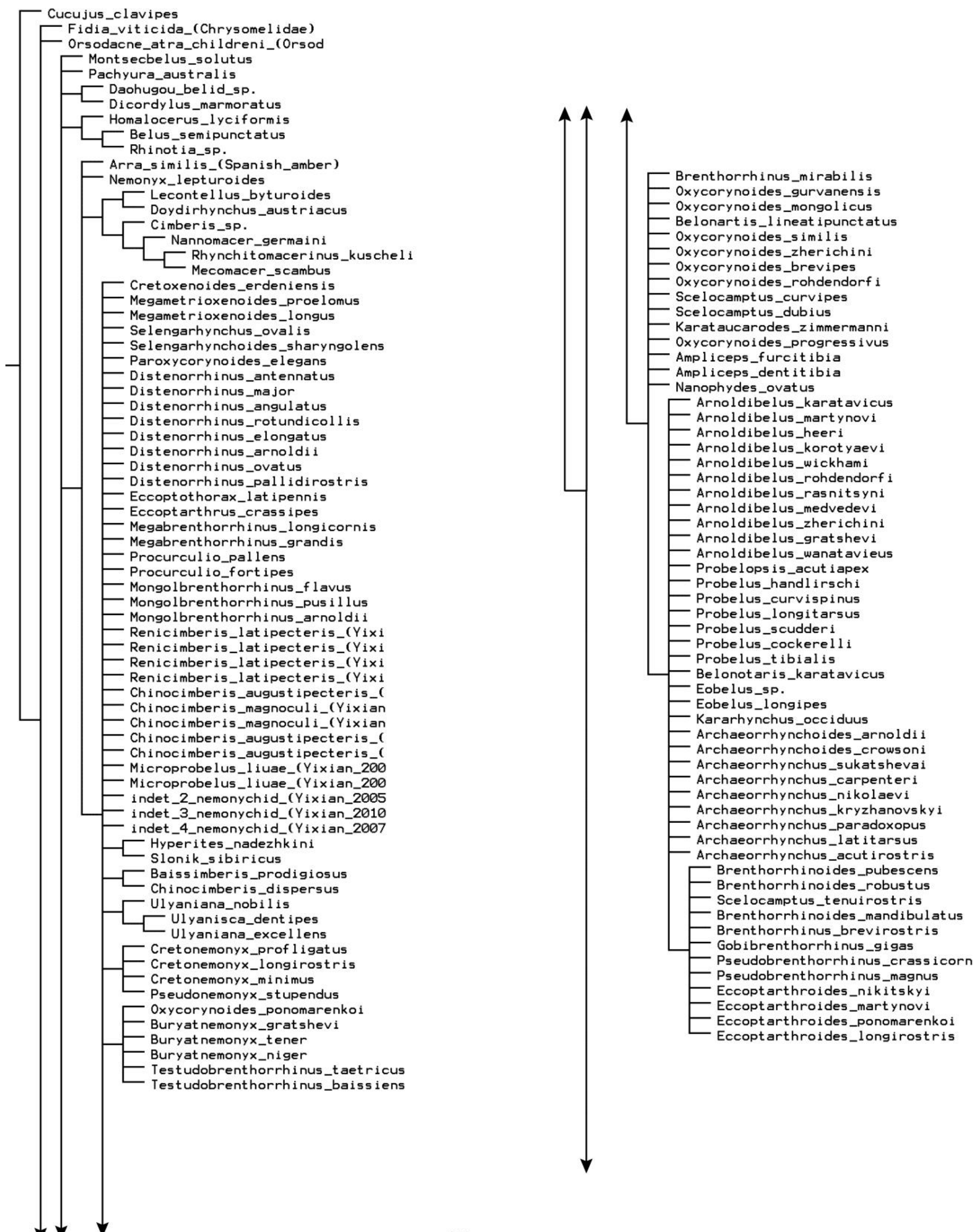

61


62

Cucujoidea +
Chrysomeloidea
Belidae
Belidae
Oxycorynidae
Anthribidae
Nemonychidae
Attelabidae
Caridae
s.l.
Caridae
s.s.
Ithyceridae
Brentidae
Apionidae +
Nanophyidae
Brachyceridae
Curculionidae s.l.


63


Molytinae +
Lixinae +
Mesoptilinae
Raymondionyminae
Cryptolarynginae
Erirhininae
Hyperinae
Cyclominae
Conoderinae
Cryptorhynchinae
Bardinae
Ceutorhynchinae
Conoderinae
Entiminae
Cossoninae
Curculioninae
Bagoinae
Scolytinae +
Platypodinae
Dryophthorinae
64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Fidia_viticida_(Chrysomelidae)
Orsodacne_atra_childreni_(Orsod
Montsecbelus_solutus
Pachyura_australis
Daohugou_belid_sp.
Dicordylus_marmoratus
Homalocerus_lyciformis
Belus_semipunctatus
Rhinotia_sp.
Arra_similis_(Spanish_amber)
Nemonyx_lepturoides
Lecontellus_byturoides
Doydirhynchus_austriacus
Cimberis_sp.
Nannomacer_germaini
Rhynchitomacerinus_kuscheli
Mecomacer_scambus
Cretoxenoides_erdeniensis
Megametrioxenoides_proelomus
Megametrioxenoides_longus
Selengarhynchus_ovalis
Selengarhynchoides_sharyngolens
Paroxycorynoides_elegans
Distenorrhinus_antennatus
Distenorrhinus_major
Distenorrhinus_angulatus
Distenorrhinus_rotundicollis
Distenorrhinus_elongatus
Distenorrhinus_arnoldii
Distenorrhinus_ovatus
Distenorrhinus_pallidirostris
Eccoptothorax_latipennis
Eccoptarthrus_crassipes
Megabrenthorrhinus_longicornis
Megabrenthorrhinus_grandis
Procurculio_pallens
Procurculio_fortipes
Mongolbrenthorrhinus_flavus
Mongolbrenthorrhinus_pusillus
Mongolbrenthorrhinus_arnoldii
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Renicimberis_latipecteris_(Yixi
Renicimberis_latipecteris_(Yixi
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Chinocimberis_augustipecteris_(
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Chinocimberis_magnoculi_(Yixian
Chinocimberis_augustipecteris_(
Chinocimberis_augustipecteris_(
Microprobelus_liuae_(Yixian_200
Microprobelus_liuae_(Yixian_200
indet_2_nemonychid_(Yixian_2005
indet_3_nemonychid_(Yixian_2010
indet_4_nemonychid_(Yixian_2007
Hyperites_nadezhkini
Slonik_sibiricus
Baissimberis_prodigiosus
Chinocimberis_dispersus
Ulyaniana_nobilis
Ulyanisca_dentipes
Ulyaniana_excellens
Cretonemonyx_profligatus
Cretonemonyx_longirostris
Cretonemonyx_minimus
Pseudonemonyx_stupendus
Oxycorynoides_ponomarenkoi
Buryatnemonyx_gratshevi
Buryatnemonyx_tener
Buryatnemonyx_niger
Testudobrenthorrhinus_taetricus
Testudobrenthorrhinus_baissiens
Brenthorrhinus_mirabilis
Oxycorynoides_gurvanensis
Oxycorynoides_mongolicus
Belonartis_lineatipunctatus
Oxycorynoides_similis
Oxycorynoides_zherichini
Oxycorynoides_brevipes
Oxycorynoides_rohdendorfi
Scelocamptus_curvipes
Scelocamptus_dubius
Karataucarodes_zimmermanni
Oxycorynoides_progressivus
Ampliceps_furcitibia
Ampliceps_dentitibia
Nanophydes_ovatus
Arnoldibelus_karatavicus
Arnoldibelus_martynovi
Arnoldibelus_heeri
Arnoldibelus_korotyaevi
Arnoldibelus_wickhami
Arnoldibelus_rohdendorfi
Arnoldibelus_rasnitsyni
Arnoldibelus_medvedevi
Arnoldibelus_zherichini
Arnoldibelus_gratshevi
Arnoldibelus_wanatavieus
Probelopsis_acutiapex
Probelus_handlirschi
Probelus_curvispinus
Probelus_longitarsus
Probelus_scudderi
Probelus_cockerelli
Probelus_tibialis
Belonotaris_karatavicus
Eobelus_sp.
Eobelus_longipes
Kararhynchus_occiduus
Archaeorrhynchoides_arnoldii
Archaeorrhynchoides_crowsoni
Archaeorrhynchus_sukatshevai
Archaeorrhynchus_carpenteri
Archaeorrhynchus_nikolaevi
Archaeorrhynchus_kryzhanovskyi
Archaeorrhynchus_paradoxopus
Archaeorrhynchus_latitarsus
Archaeorrhynchus_acutirostris
Brenthorrhinoides_pubescens
Brenthorrhinoides_robustus
Scelocamptus_tenuirostris
Brenthorrhinoides_mandibulatus
Brenthorrhinus_brevirostris
Gobibrenthorrhinus_gigas
Pseudobrenthorrhinus_crassicorn
Pseudobrenthorrhinus_magnus
Eccoptarthroides_nikitskyi
Eccoptarthroides_martynovi
Eccoptarthroides_ponomarenkoi
Eccoptarthroides_longirostris

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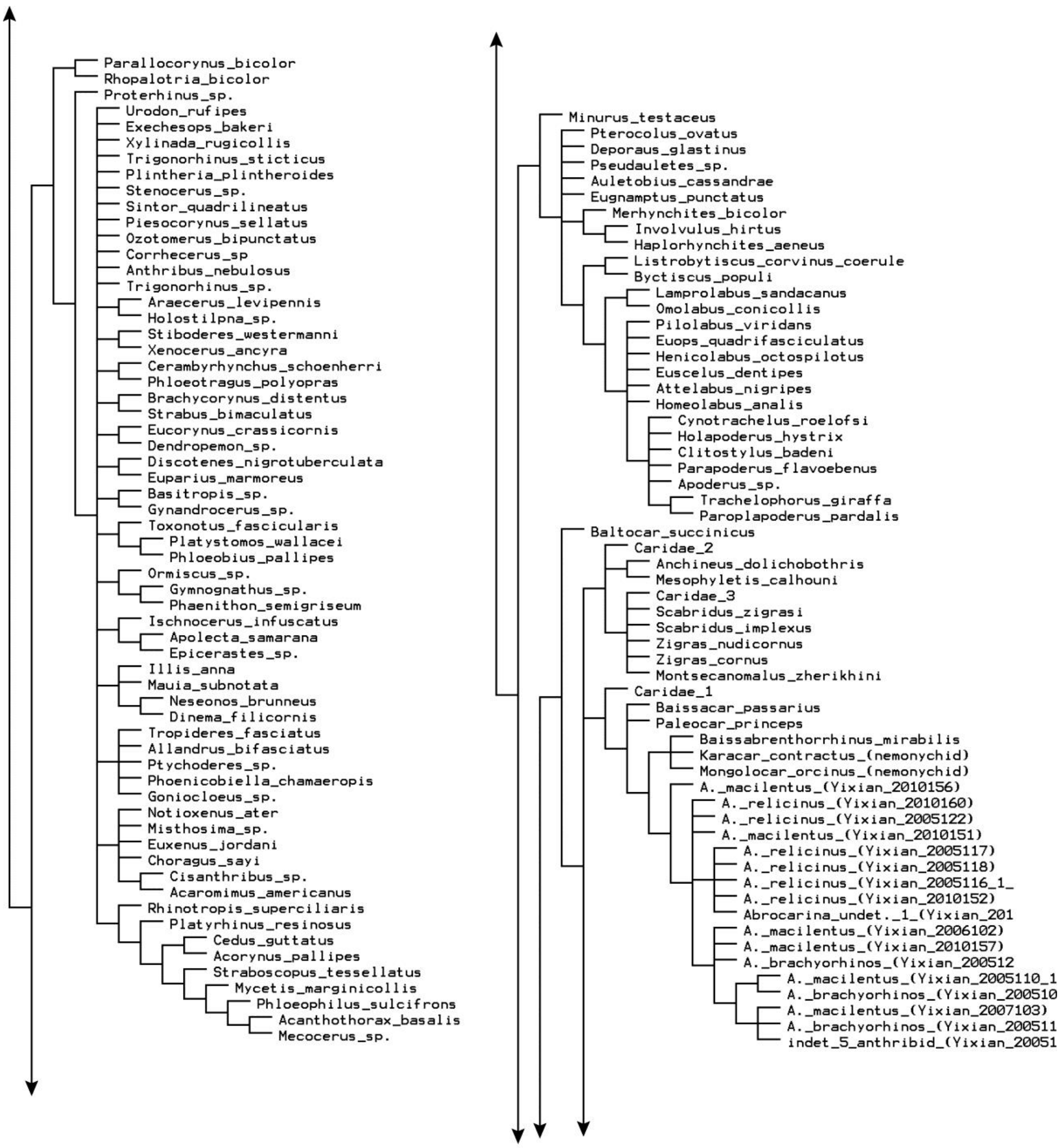

Parallocorynus_bicolor
Rhopalotria_bicolor
Proterhinus_sp.
Urodon_rufipes
Exechesops_bakeri
Xylinada_rugicollis
Trigonorhinus_sticticus
Plintheria_plintheroides
Stenocerus_sp.
Sintor_quadrilineatus
Piesocorynus_sellatus
Ozotomerus_bipunctatus
Corrhecerus_sp
Anthribus_nebulosus
Trigonorhinus_sp.
Araecerus_levipennis
Holostilpna_sp.
Stiboderes_westermanni
Xenocerus_ancyra
Cerambyrhynchus_schoenherri
Phloeotragus_polyopras
Brachycorynus_distentus
Strabus_bimaculatus
Eucorynus_crassicornis
Dendropemon_sp.
Discotenes_nigrotuberculata
Euparius_marmoreus
Basitropis_sp.
Gynandrocerus_sp.
Toxonotus_fascicularis
Platystomos_wallacei
Phloeobius_pallipes
Ormiscus_sp.
Gymnognathus_sp.
Phaenithon_semigriseum
Ischnocerus_infuscatus
Apolecta_samarana
Epicerastes_sp.
Illis_anna
Mauia_subnotata
Neseonos_brunneus
Dinema_filicornis
Tropideres_fasciatus
Allandrus_bifasciatus
Ptychoderes_sp.
Phoenicobiella_chamaeropis
Goniocloeus_sp.
Notioxenus_ater
Misthosima_sp.
Euxenus_jordani
Choragus_sayi
Cisanthribus_sp.
Acaromimus_americanus
Rhinotropis_superciliaris
Platyrhinus_resinosus
Cedus_guttatus
Acorynus_pallipes
Straboscopus_tessellatus
Mycetis_marginicollis
Phloeophilus_sulcifrons
Acanthothorax_basalis
Mecocerus_sp.
Minurus_testaceus
Pterocolus_ovatus
Deporaus_glastinus
Pseudauletes_sp.
Auletobius_cassandrae
Eugnamptus_punctatus
Merhynchites_bicolor
Involvulus_hirtus
Haplorhynchites_aeneus
Listrobytiscus_corvinus_coerule
Byctiscus_populi
Lamprolabus_sandacanus
Omolabus_conicollis
Pilolabus_viridans
Euops_quadrifasciculatus
Henicolabus_octospilotus
Euscelus_dentipes
Attelabus_nigripes
Homeolabus_analis
Cynotrachelus_roelofsi
Holapoderus_hystrix
Clitostylus_badeni
Parapoderus_flavoebenus
Apoderus_sp.
Trachelophorus_giraffa
Paroplapoderus_pardalis
Baltocar_succinicus
Caridae_2
Anchineus_dolichobothris
Mesophyletis_calhouni
Caridae_3
Scabridus_zigrasi
Scabridus_implexus
Zigras_nudicornus
Zigras_cornus
Montsecanomalus_zherikhini
Caridae_1
Baissacar_passarius
Paleocar_princeps
Baissabrenthorrhinus_mirabilis
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Mongolocar_orcinus_(nemonychid)
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A._relicinus_(Yixian_2010160)
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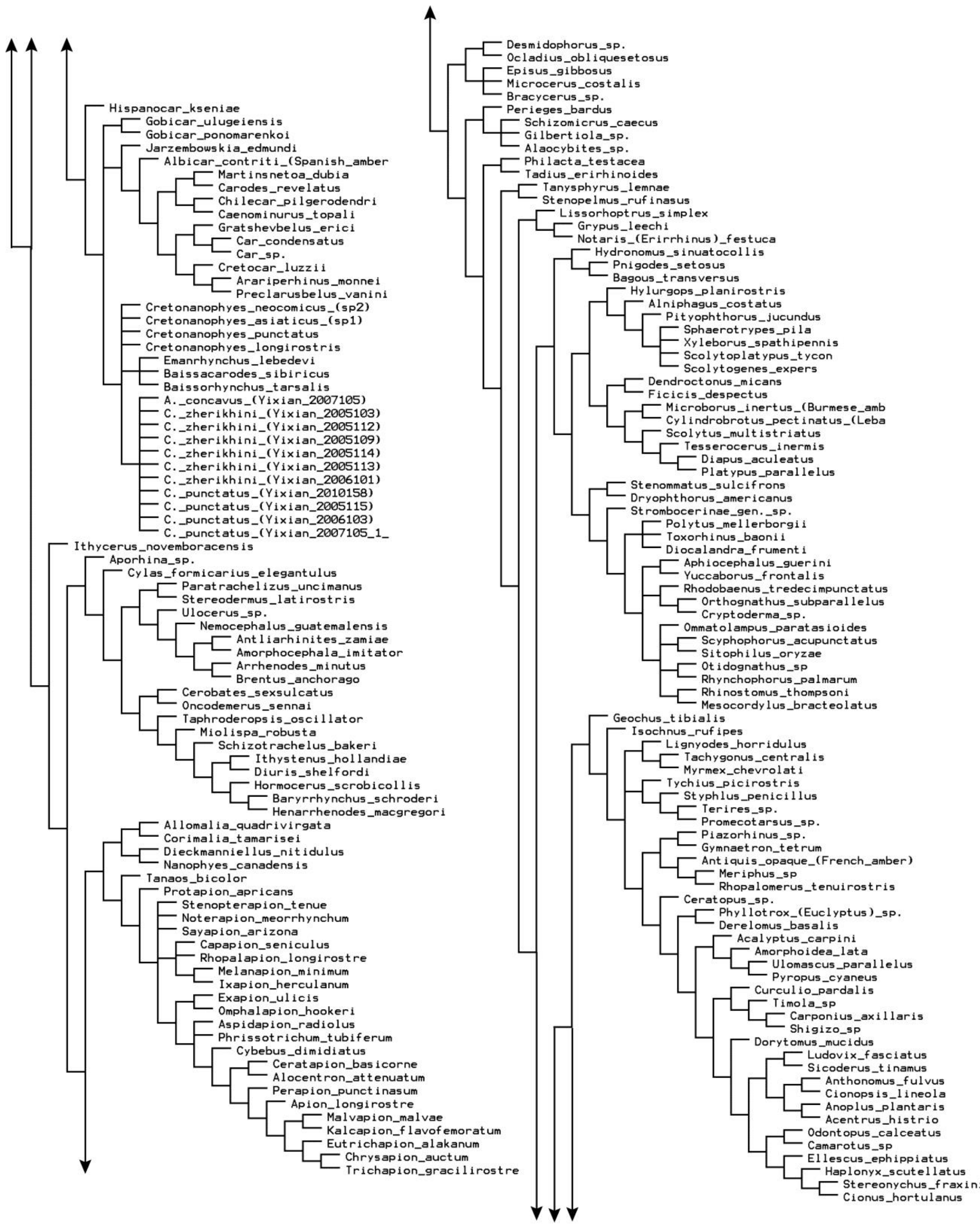
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Gobicar_ponomarenkoi
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Carodes_revelatus
Chilecar_pilgerodendri
Caenominurus_topali
Gratshevbelus_erici
Car_condensatus
Car_sp.
Cretocar_luzzii
Arariperhinus_monnei
Preclarusbelus_vanini
Cretonanophyes_neocomicus_(sp2)
Cretonanophyes_asiaticus_(sp1)
Cretonanophyes_punctatus
Cretonanophyes_longirostris
Emanrhynchus_lebedevi
Baissacarodes_sibiricus
Baissorhynchus_tarsalis
A._concavus_(Yixian_2007105)
C._zherikhini_(Yixian_2005103)
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C._punctatus_(Yixian_2005115)
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Aporhina_sp.
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Stereodermus_latirostris
Ulocerus_sp.
Nemocephalus_guatemalensis
Antliarhinites_zamiae
Amorphocephala_imitator
Arrhenodes_minutus
Brentus_anchorago
Cerobates_sexsulcatus
Oncodemerus_sennai
Taphroderopsis_oscillator
Miolispa_robusta
Schizotrachelus_bakeri
Ithystenus_hollandiae
Diuris_shelfordi
Hormocerus_scrobicollis
Baryrrhynchus_schroderi
Henarrhenodes_macgregori
Allomalia_quadrivirgata
Corimalia_tamarisei
Dieckmanniellus_nitidulus
Nanophyes_canadensis
Tanaos_bicolor
Protapion_apricans
Stenopterapion_tenue
Noterapion_meorrhynchum
Sayapion_arizona
Capapion_seniculus
Rhopalapion_longirostre
Melanapion_minimum
Ixapion_herculanum
Exapion_ulicis
Omphalapion_hookeri
Aspidapion_radiolus
Phrissotrichum_tubiferum
Cybebus_dimidiatus
Ceratapion_basicorne
Alocentron_attenuatum
Perapion_punctinasum
Apion_longirostre
Malvapion_malvae
Kalcapion_flavofemoratum
Eutrichapion_alakanum
Chrysapion_auctum
Trichapion_gracilirostre
Desmidophorus_sp.
Ocladius_obliquesetosus
Episus_gibbosus
Microcerus_costalis
Bracycerus_sp.
Perieges_bardus
Schizomicrus_caecus
Gilbertiola_sp.
Alaocybites_sp.
Philacta_testacea
Tadius_erirhinoides
Tanysphyrus_lemnae
Stenopelmus_rufinasus
Lissorhoptrus_simplex
Grypus_leechi
Notaris_(Erirrhinus)_festuca
Hydronomus_sinuatocollis
Pnigodes_setosus
Bagous_transversus
Hylurgops_planirostris
Alniphagus_costatus
Pityophthorus_jucundus
Sphaerotrypes_pila
Xyleborus_spathipennis
Scolytoplatypus_tycon
Scolytogenes_expers
Dendroctonus_micans
Ficicis_despectus
Microborus_inertus_(Burmese_amb
Cylindrobrotus_pectinatus_(Leba
Scolytus_multistriatus
Tesserocerus_inermis
Diapus_aculeatus
Platypus_parallelus
Stenommatus_sulcifrons
Dryophthorus_americanus
Strombocerinae_gen._sp.
Polytus_mellerborgii
Toxorhinus_baonii
Diocalandra_frumenti
Aphiocephalus_guerini
Yuccaborus_frontalis
Rhodobaenus_tredecimpunctatus
Orthognathus_subparallelus
Cryptoderma_sp.
Ommatolampus_paratasioides
Scyphophorus_acupunctatus
Sitophilus_oryzae
Otidognathus_sp
Rhynchophorus_palmarum
Rhinostomus_thompsoni
Mesocordylus_bracteolatus
Geochus_tibialis
Isochnus_rufipes
Lignyodes_horridulus
Tachygonus_centralis
Myrmex_chevrolati
Tychius_picirostris
Styphlus_penicillus
Terires_sp.
Promecotarsus_sp.
Piazorhinus_sp.
Gymnaetron_tetrum
Antiquis_opaque_(French_amber)
Meriphus_sp
Rhopalomerus_tenuirostris
Ceratopus_sp.
Phyllotrox_(Euclyptus)_sp.
Derelomus_basalis
Acalyptus_carpini
Amorphoidea_lata
Ulomascus_parallelus
Pyropus_cyaneus
Curculio_pardalis
Timola_sp
Carponius_axillaris
Shigizo_sp
Dorytomus_mucidus
Ludovix_fasciatus
Sicoderus_tinamus
Anthonomus_fulvus
Cionopsis_lineola
Anoplus_plantaris
Acentrus_histrio
Odontopus_calceatus
Camarotus_sp
Ellescus_ephippiatus
Haplonyx_scutellatus
Stereonychus_fraxini
Cionus_hortulanus

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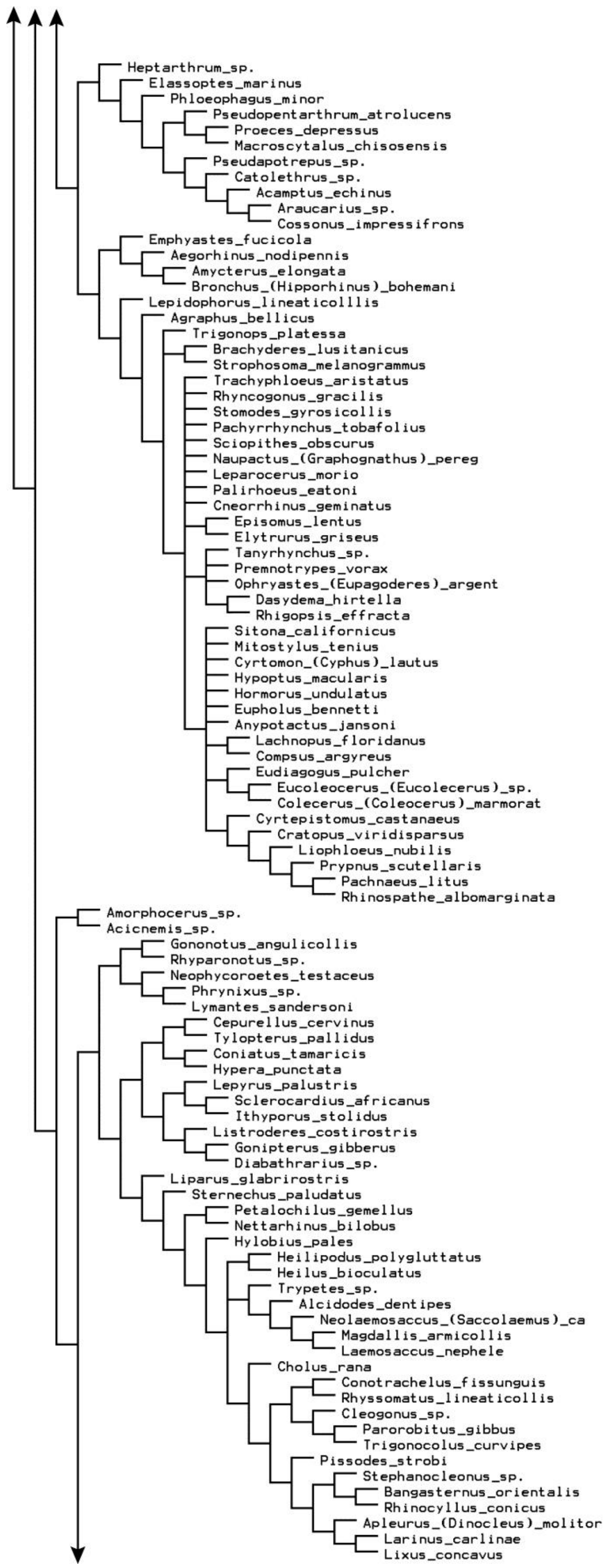
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Pseudopentarthrum_atrolucens
Proeces_depressus
Macroscytalus_chisosensis
Pseudapotrepus_sp.
Catolethrus_sp.
Acamptus_echinus
Araucarius_sp.
Cossonus_impressifrons
Emphyastes_fucicola
Aegorhinus_nodipennis
Amycterus_elongata
Bronchus_(Hipporhinus)_bohemani
Lepidophorus_lineaticolllis
Agraphus_bellicus
Trigonops_platessa
Brachyderes_lusitanicus
Strophosoma_melanogrammus
Trachyphloeus_aristatus
Rhyncogonus_gracilis
Stomodes_gyrosicollis
Pachyrrhynchus_tobafolius
Sciopithes_obscurus
Naupactus_(Graphognathus)_pereg
Leparocerus_morio
Palirhoeus_eatoni
Cneorrhinus_geminatus
Episomus_lentus
Elytrurus_griseus
Tanyrhynchus_sp.
Premnotrypes_vorax
Ophryastes_(Eupagoderes)_argent
Dasydema_hirtella
Rhigopsis_effracta
Sitona_californicus
Mitostylus_tenius
Cyrtomon_(Cyphus)_lautus
Hypoptus_macularis
Hormorus_undulatus
Eupholus_bennetti
Anypotactus_jansoni
Lachnopus_floridanus
Compsus_argyreus
Eudiagogus_pulcher
Eucoleocerus_(Eucolecerus)_sp.
Colecerus_(Coleocerus)_marmorat
Cyrtepistomus_castanaeus
Cratopus_viridisparsus
Liophloeus_nubilis
Prypnus_scutellaris
Pachnaeus_litus
Rhinospathe_albomarginata
Amorphocerus_sp.
Acicnemis_sp.
Gononotus_angulicollis
Rhyparonotus_sp.
Neophycoroetes_testaceus
Phrynixus_sp.
Lymantes_sandersoni
Cepurellus_cervinus
Tylopterus_pallidus
Coniatus_tamaricis
Hypera_punctata
Lepyrus_palustris
Sclerocardius_africanus
Ithyporus_stolidus
Listroderes_costirostris
Gonipterus_gibberus
Diabathrarius_sp.
Liparus_glabrirostris
Sternechus_paludatus
Petalochilus_gemellus
Nettarhinus_bilobus
Hylobius_pales
Heilipodus_polygluttatus
Heilus_bioculatus
Trypetes_sp.
Alcidodes_dentipes
Neolaemosaccus_(Saccolaemus)_ca
Magdallis_armicollis
Laemosaccus_nephele
Cholus_rana
Conotrachelus_fissunguis
Rhyssomatus_lineaticollis
Cleogonus_sp.
Parorobitus_gibbus
Trigonocolus_curvipes
Pissodes_strobi
Stephanocleonus_sp.
Bangasternus_orientalis
Rhinocyllus_conicus
Apleurus_(Dinocleus)_molitor
Larinus_carlinae
Lixus_concavus

Guioperus_trifasciatus
Gerstaeckeria_lecontei
Eurhoptus_sp.
Torneuma_subpanum
Strongylopterus_ovatus
Psepholax_humilis
Cophes_obtenus
Coelosternus_sp.
Cryptorhynchus_lapathi
Camptorhinus_sp.
Mechistocerus_sp.
Aedemonus_erichsoni
Cratosomus_"punctulatus"
Trichodocerus_sp.
Lobotrachelus_troglodytes
Mecopus_trilineatus
Acoptus_suturalis
Metialma_straminea
Balanogastris_kolae
Telephae_oculata
Hoplocopturus_sp.
Cylindrocopturus_adspersus
Cylindrocopturus_operculatus
Cyllophorus_fausciatus
Campyloscelus_westermanni
Arachnobas_gazella
Eisonyx_crassipes
Calandrinus_grandicollis
Xystus_ater
Diorymeropsis_xanthoxyli
Baris_torquata
Thanius_sp.
Pycnobaris_pruinosa
Barinus_bivittatus
Nicentrus_grossulus
Torcus_nigrinus
Limnobaris_bicincta
Anthinobaris_dispilota
Sibariops_concurrens
Peridinetus_irroratus
Madopterus_talpa
Lioxyonyx_fausti
Anthypurinus_haloxylicola
Cyphosenus_citricola
Auleutes_epilobii
Coeliodes_rana
Dieckmannius_sexnotatus
Xenysmoderodes_sasajii
Mecysmoderes_euglyptus
Mononychus_punctumalbum
Augustinus_comes
Ceutorhynchus_nitidulus
Cardipennis_sulcithorax
Amalus_scortillum
Homorosoma_asperum
Rhinoncus_perpendicularis
Pelenomus_roelofsi
Rutidosoma_globulus
Scleropterus_serratus


Cucujus_clavipes
Fidia_viticida_(Chrysomelidae)
Orsodacne_atra_childreni_(Orsod
Arra_similis_(Spanish_amber)
Nemonyx_lepturoides
Lecontellus_byturoides
Doydirhynchus_austriacus
Cimberis_sp.
Nannomacer_germaini
Rhynchitomacerinus_kuscheli
Mecomacer_scambus
Homalocerus_lyciformis
Belus_semipunctatus
Rhinotia_sp.
Montsecbelus_solutus
Pachyura_australis
Daohugou_belid_sp.
Dicordylus_marmoratus
Parallocorynus_bicolor
Rhopalotria_bicolor
Proterhinus_sp.
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Araecerus_levipennis
Holostilpna_sp.
Ormiscus_sp.
Gymnognathus_sp.
Phaenithon_semigriseum
Xylinada_rugicollis
Tropideres_fasciatus
Phoenicobiella_chamaeropis
Goniocloeus_sp.
Allandrus_bifasciatus
Ptychoderes_sp.
Anthribus_nebulosus
Trigonorhinus_sp.
Discotenes_nigrotuberculata
Euparius_marmoreus
Ozotomerus_bipunctatus
Corrhecerus_sp
Brachycorynus_distentus
Strabus_bimaculatus
Basitropis_sp.
Gynandrocerus_sp.
Eucorynus_crassicornis
Dendropemon_sp.
Ischnocerus_infuscatus
Apolecta_samarana
Epicerastes_sp.
Illis_anna
Mauia_subnotata
Neseonos_brunneus
Dinema_filicornis
Notioxenus_ater
Euxenus_jordani
Choragus_sayi
Misthosima_sp.
Cisanthribus_sp.
Acaromimus_americanus
Urodon_rufipes
Toxonotus_fascicularis
Platystomos_wallacei
Phloeobius_pallipes
Stiboderes_westermanni
Xenocerus_ancyra
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Phloeotragus_polyopras
Stenocerus_sp.
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Sintor_quadrilineatus
Rhinotropis_superciliaris
Platyrhinus_resinosus
Cedus_guttatus
Acorynus_pallipes
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Acanthothorax_basalis
Mecocerus_sp.

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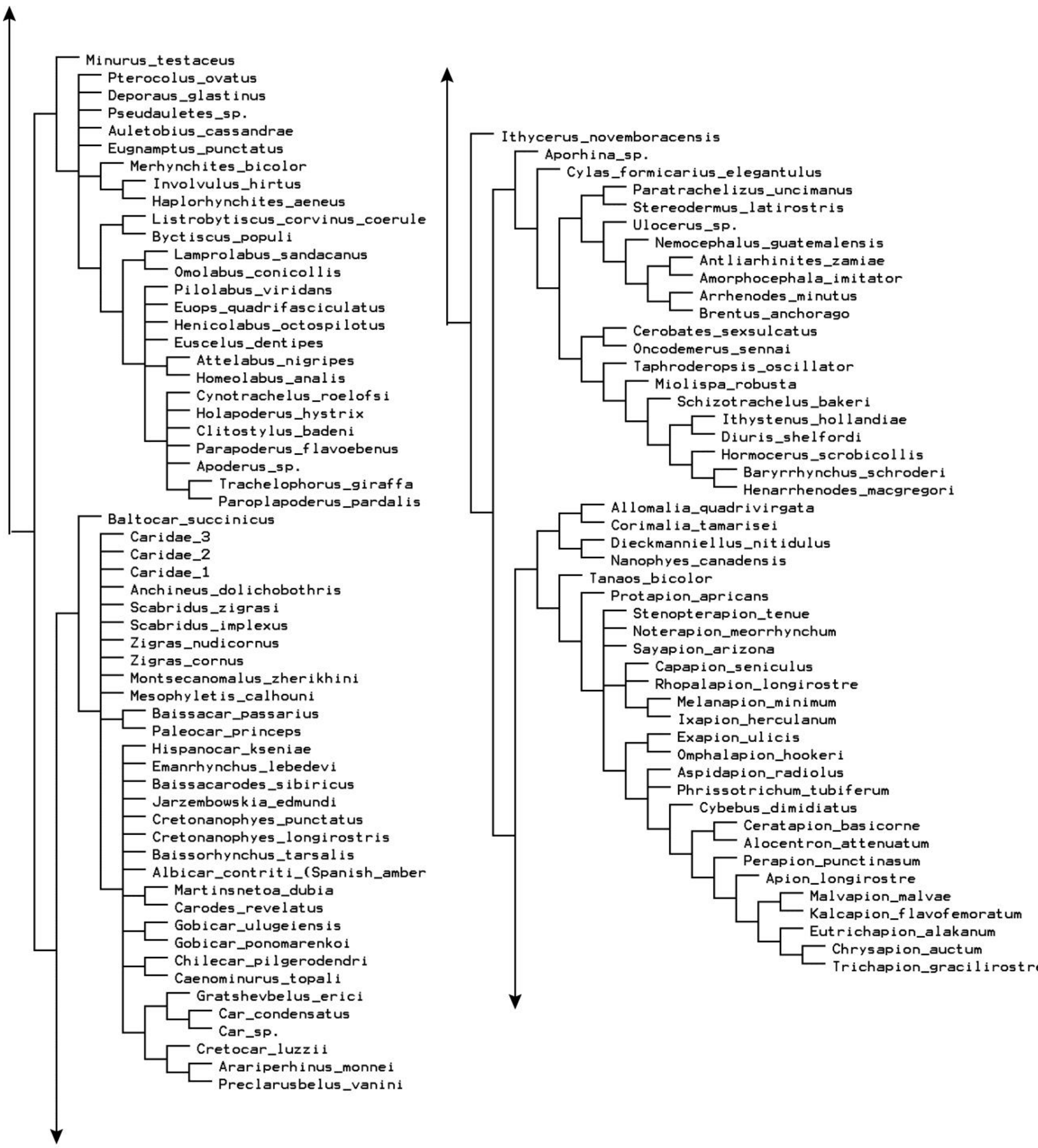
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Pterocolus_ovatus
Deporaus_glastinus
Pseudauletes_sp.
Auletobius_cassandrae
Eugnamptus_punctatus
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Involvulus_hirtus
Haplorhynchites_aeneus
Listrobytiscus_corvinus_coerule
Byctiscus_populi
Lamprolabus_sandacanus
Omolabus_conicollis
Pilolabus_viridans
Euops_quadrifasciculatus
Henicolabus_octospilotus
Euscelus_dentipes
Attelabus_nigripes
Homeolabus_analis
Cynotrachelus_roelofsi
Holapoderus_hystrix
Clitostylus_badeni
Parapoderus_flavoebenus
Apoderus_sp.
Trachelophorus_giraffa
Paroplapoderus_pardalis
Baltocar_succinicus
Caridae_3
Caridae_2
Caridae_1
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Scabridus_zigrasi
Scabridus_implexus
Zigras_nudicornus
Zigras_cornus
Montsecanomalus_zherikhini
Mesophyletis_calhouni
Baissacar_passarius
Paleocar_princeps
Hispanocar_kseniae
Emanrhynchus_lebedevi
Baissacarodes_sibiricus
Jarzembowskia_edmundi
Cretonanophyes_punctatus
Cretonanophyes_longirostris
Baissorhynchus_tarsalis
Albicar_contriti_(Spanish_amber
Martinsnetoa_dubia
Carodes_revelatus
Gobicar_ulugeiensis
Gobicar_ponomarenkoi
Chilecar_pilgerodendri
Caenominurus_topali
Gratshevbelus_erici
Car_condensatus
Car_sp.
Cretocar_luzzii
Arariperhinus_monnei
Preclarusbelus_vanini
Ithycerus_novemboracensis
Aporhina_sp.
Cylas_formicarius_elegantulus
Paratrachelizus_uncimanus
Stereodermus_latirostris
Ulocerus_sp.
Nemocephalus_guatemalensis
Antliarhinites_zamiae
Amorphocephala_imitator
Arrhenodes_minutus
Brentus_anchorago
Cerobates_sexsulcatus
Oncodemerus_sennai
Taphroderopsis_oscillator
Miolispa_robusta
Schizotrachelus_bakeri
Ithystenus_hollandiae
Diuris_shelfordi
Hormocerus_scrobicollis
Baryrrhynchus_schroderi
Henarrhenodes_macgregori
Allomalia_quadrivirgata
Corimalia_tamarisei
Dieckmanniellus_nitidulus
Nanophyes_canadensis
Tanaos_bicolor
Protapion_apricans
Stenopterapion_tenue
Noterapion_meorrhynchum
Sayapion_arizona
Capapion_seniculus
Rhopalapion_longirostre
Melanapion_minimum
Ixapion_herculanum
Exapion_ulicis
Omphalapion_hookeri
Aspidapion_radiolus
Phrissotrichum_tubiferum
Cybebus_dimidiatus
Ceratapion_basicorne
Alocentron_attenuatum
Perapion_punctinasum
Apion_longirostre
Malvapion_malvae
Kalcapion_flavofemoratum
Eutrichapion_alakanum
Chrysapion_auctum
Trichapion_gracilirostre

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Desmidophorus_sp.
Ocladius_obliquesetosus
Episus_gibbosus
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Bracycerus_sp.
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Pnigodes_setosus
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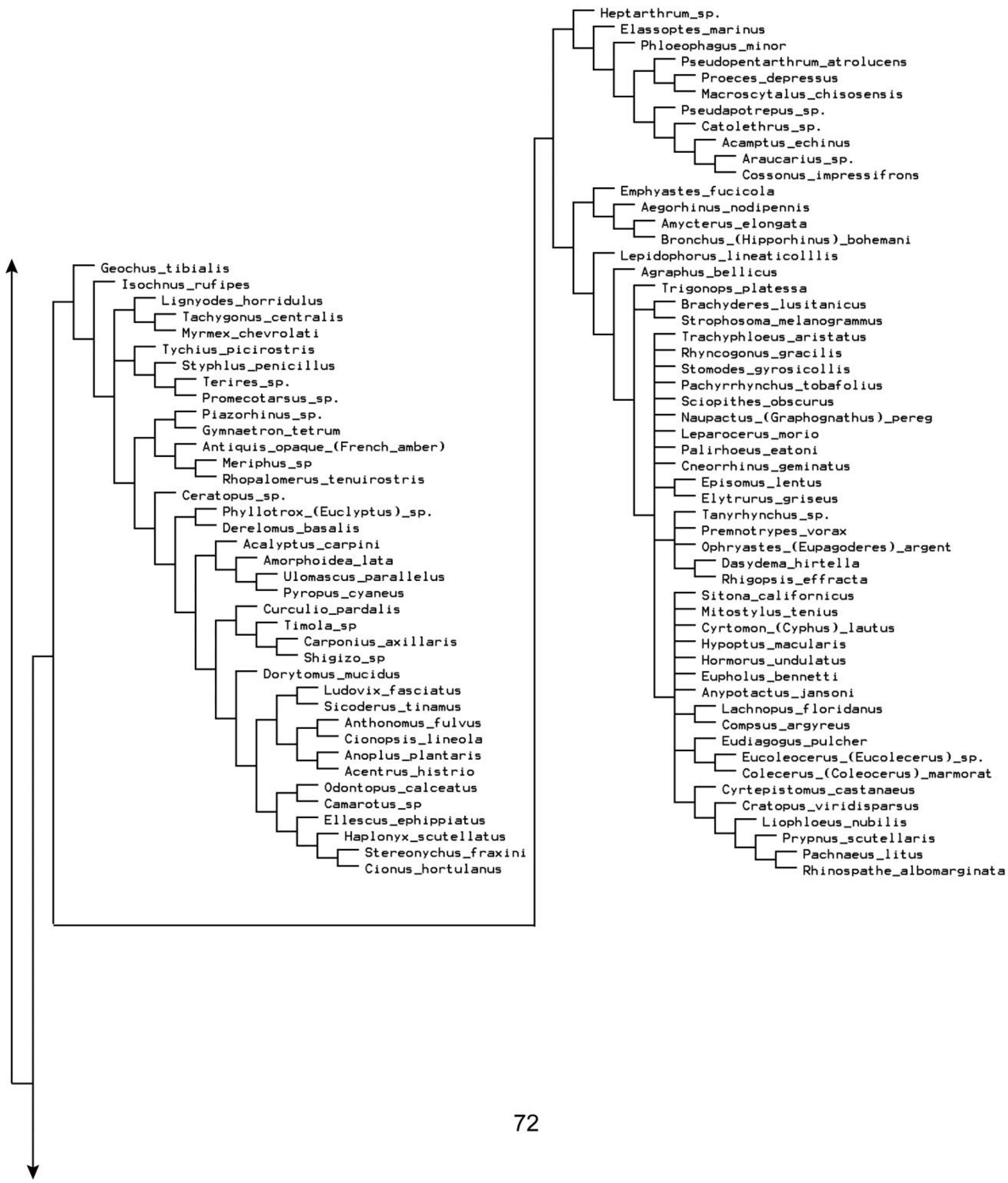
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Sciopithes_obscurus
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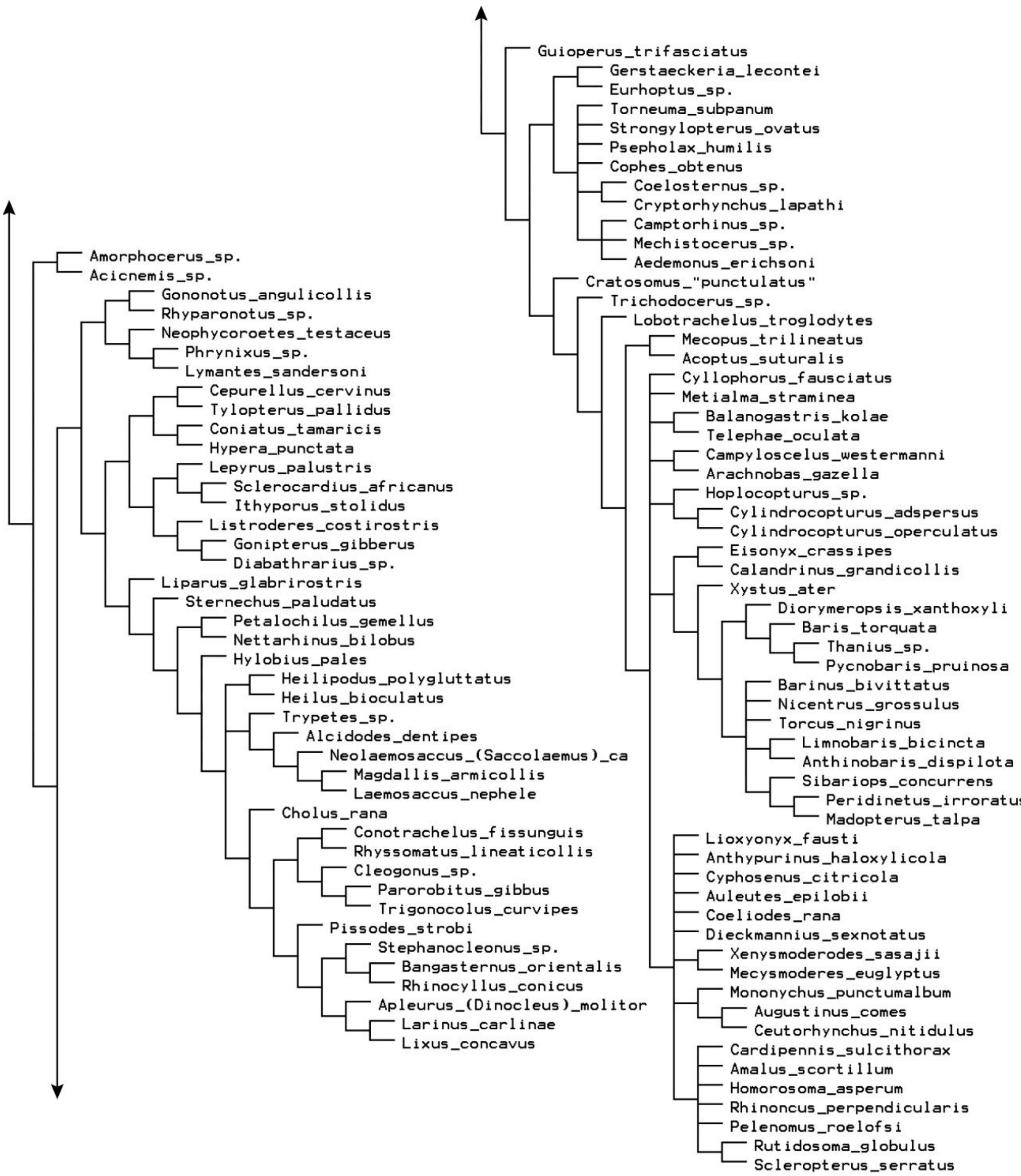
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Trypetes_sp.
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Conotrachelus_fissunguis
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Pissodes_strobi
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Bangasternus_orientalis
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Guioperus_trifasciatus
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Torneuma_subpanum
Strongylopterus_ovatus
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Cophes_obtenus
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Cratosomus_"punctulatus"
Trichodocerus_sp.
Lobotrachelus_troglodytes
Mecopus_trilineatus
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Campyloscelus_westermanni
Arachnobas_gazella
Hoplocopturus_sp.
Cylindrocopturus_adspersus
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Eisonyx_crassipes
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Xystus_ater
Diorymeropsis_xanthoxyli
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Pycnobaris_pruinosa
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Limnobaris_bicincta
Anthinobaris_dispilota
Sibariops_concurrens
Peridinetus_irroratus
Madopterus_talpa
Lioxyonyx_fausti
Anthypurinus_haloxylicola
Cyphosenus_citricola
Auleutes_epilobii
Coeliodes_rana
Dieckmannius_sexnotatus
Xenysmoderodes_sasajii
Mecysmoderes_euglyptus
Mononychus_punctumalbum
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Ceutorhynchus_nitidulus
Cardipennis_sulcithorax
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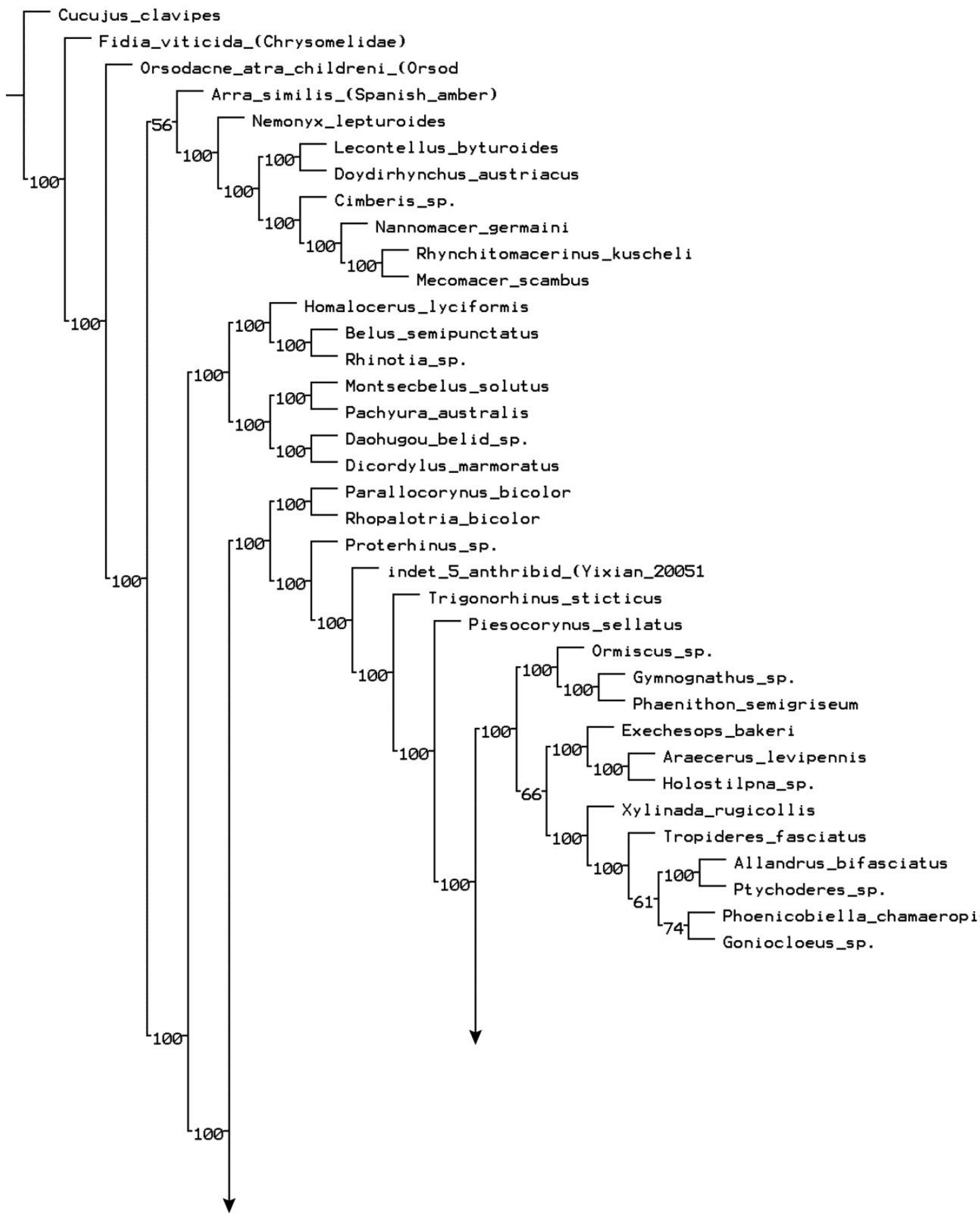
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Dicordylus_marmoratus
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indet_5_anthribid_(Yixian_20051
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Piesocorynus_sellatus
Ormiscus_sp.
Gymnognathus_sp.
Phaenithon_semigriseum
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Araecerus_levipennis
Holostilpna_sp.
Xylinada_rugicollis
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56
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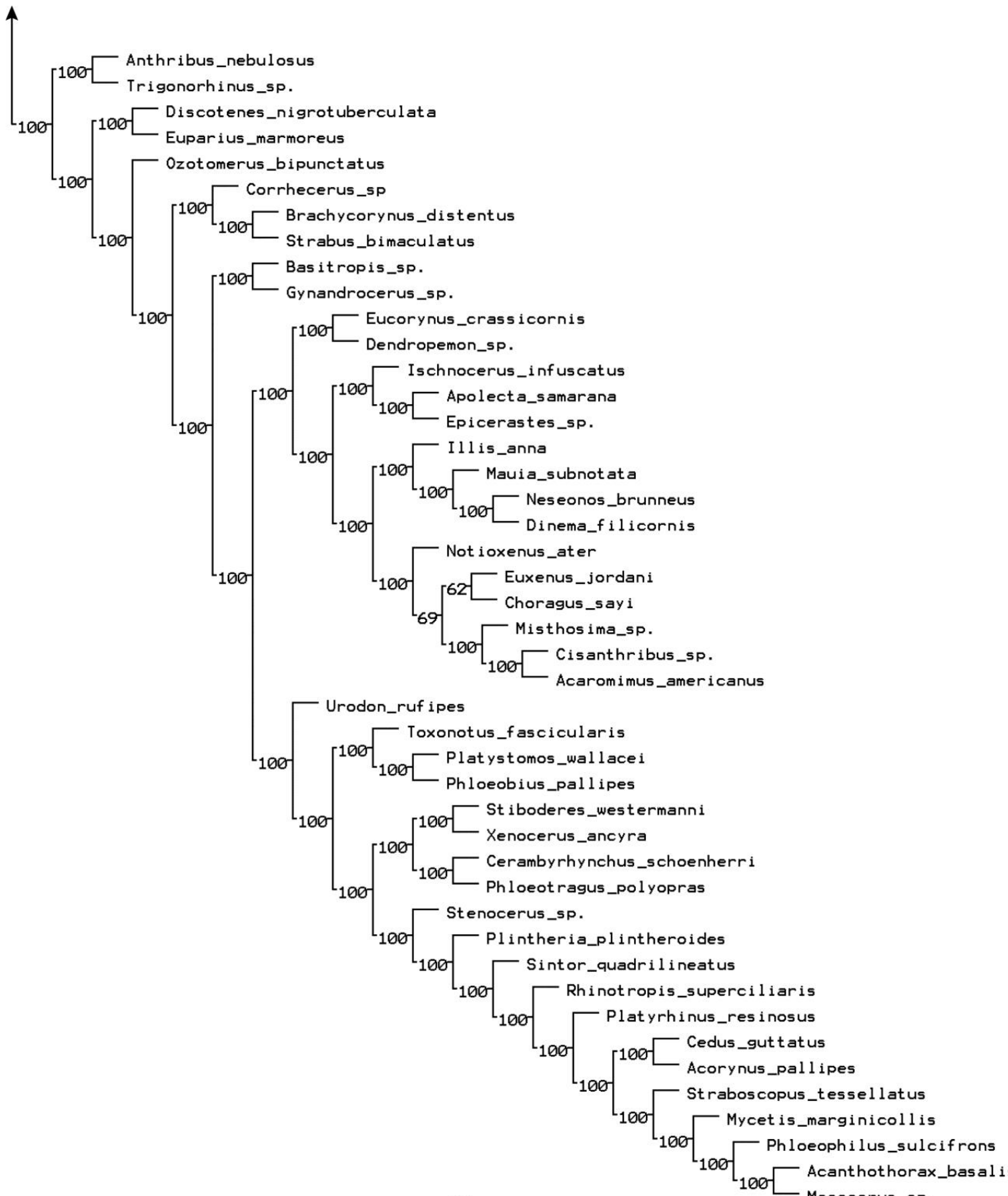
61
74
66

74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Strabus_bimaculatus
Basitropis_sp.
Gynandrocerus_sp.
Eucorynus_crassicornis
Dendropemon_sp.
Ischnocerus_infuscatus
Apolecta_samarana
Epicerastes_sp.
Illis_anna
Mauia_subnotata
Neseonos_brunneus
Dinema_filicornis
Notioxenus_ater
Euxenus_jordani
Choragus_sayi
Misthosima_sp.
Cisanthribus_sp.
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Toxonotus_fascicularis
Platystomos_wallacei
Phloeobius_pallipes
Stiboderes_westermanni
Xenocerus_ancyra
Cerambyrhynchus_schoenherri
Phloeotragus_polyopras
Stenocerus_sp.
Plintheria_plintheroides
Sintor_quadrilineatus
Rhinotropis_superciliaris
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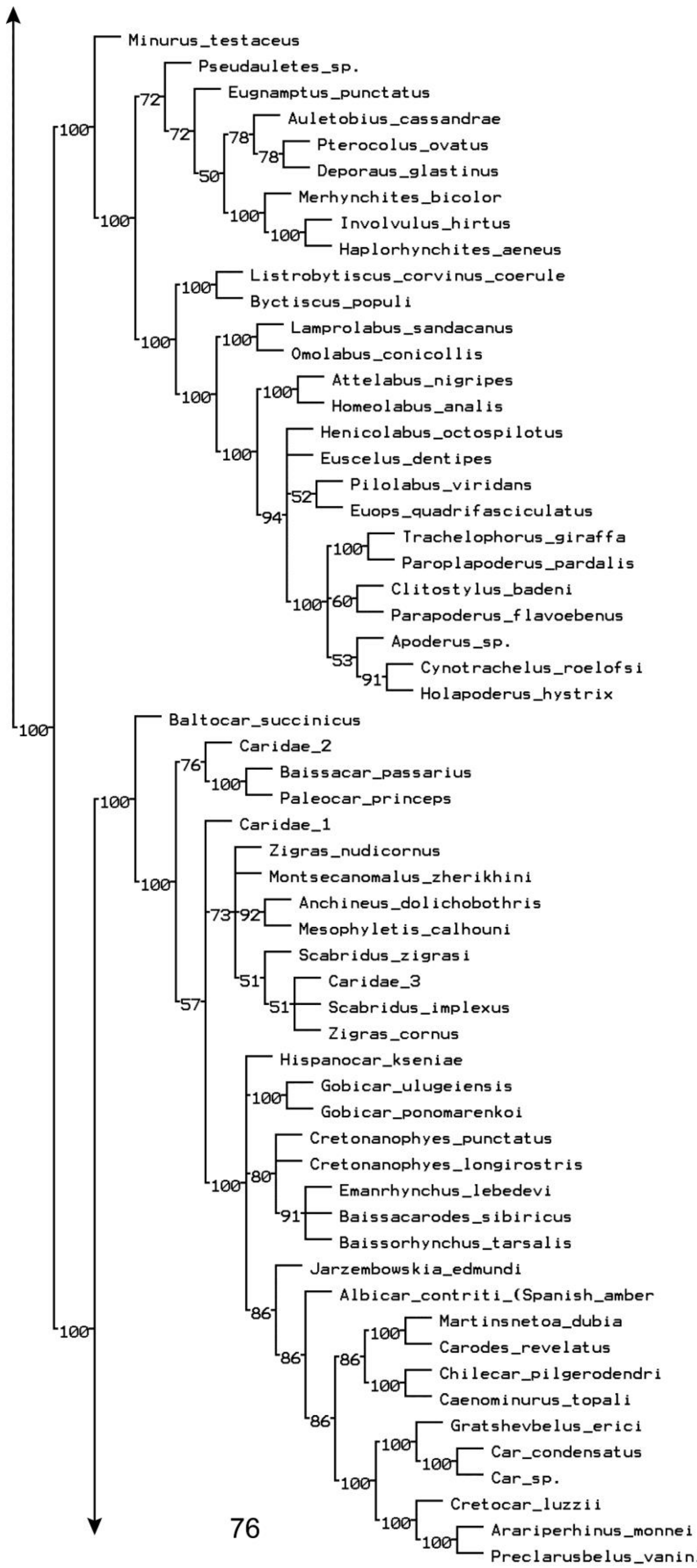
75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Euscelus_dentipes
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Anchineus_dolichobothris
Mesophyletis_calhouni
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Zigras_cornus
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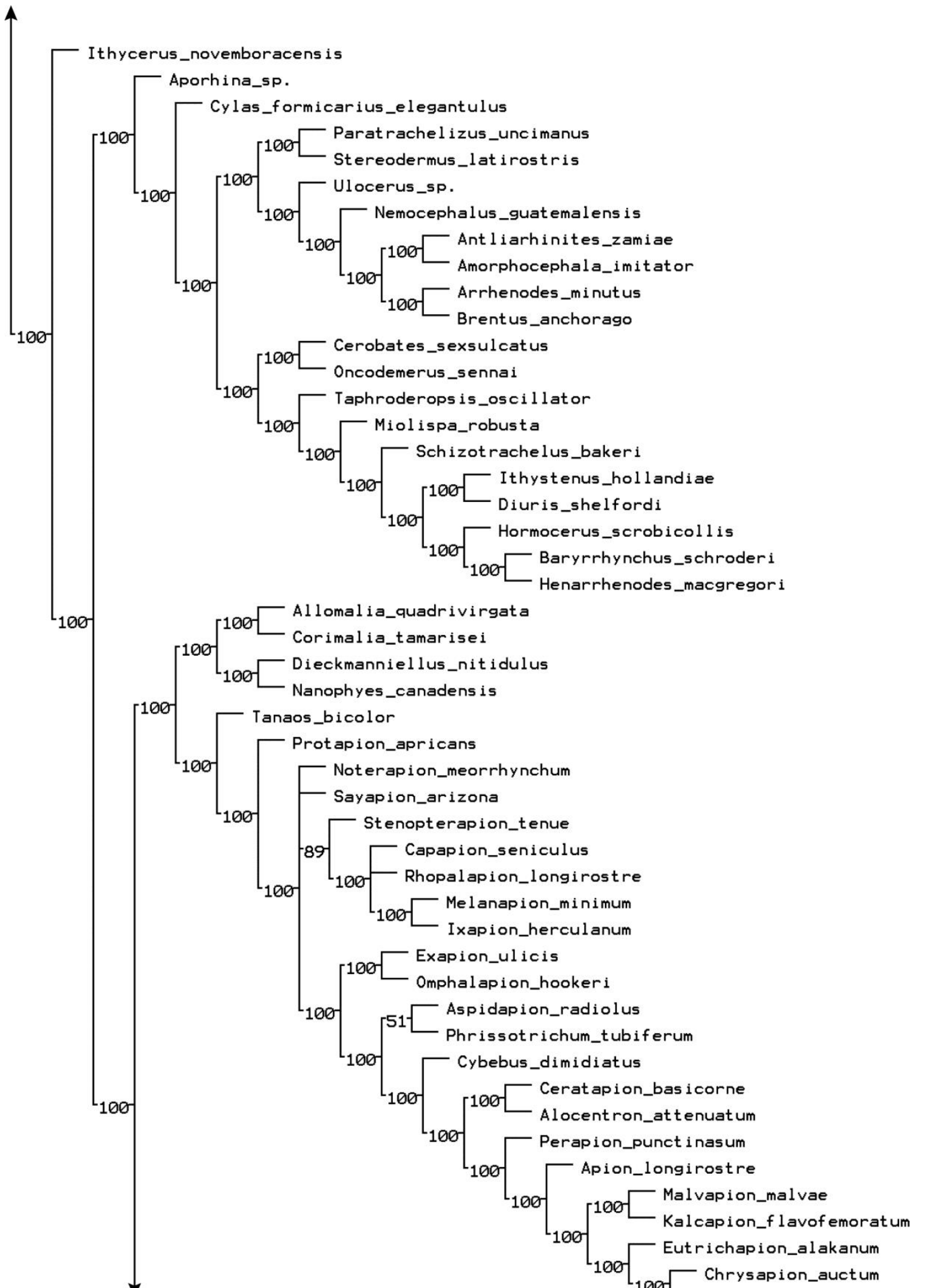
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Dieckmanniellus_nitidulus
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Sayapion_arizona
Stenopterapion_tenue
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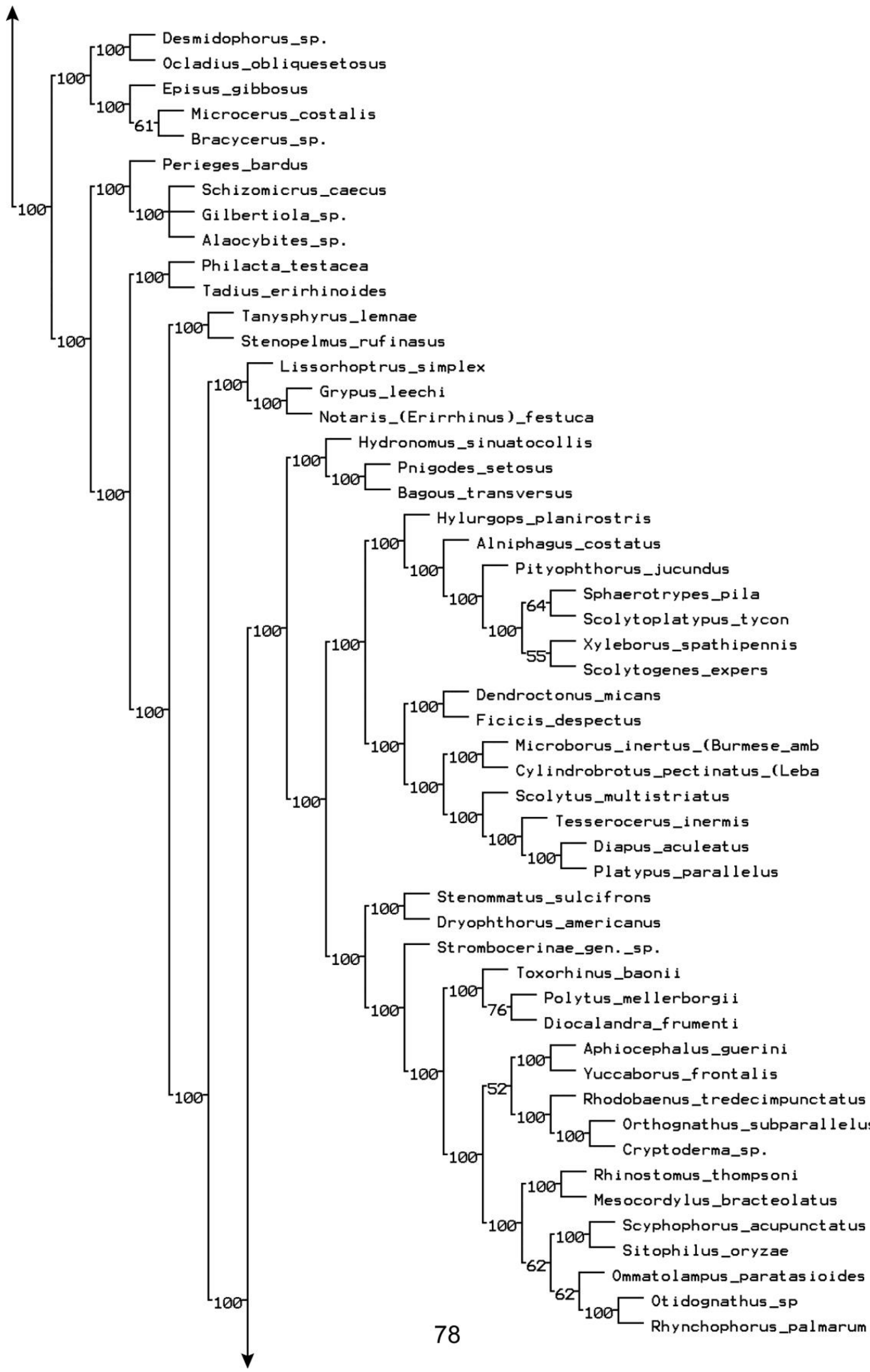
77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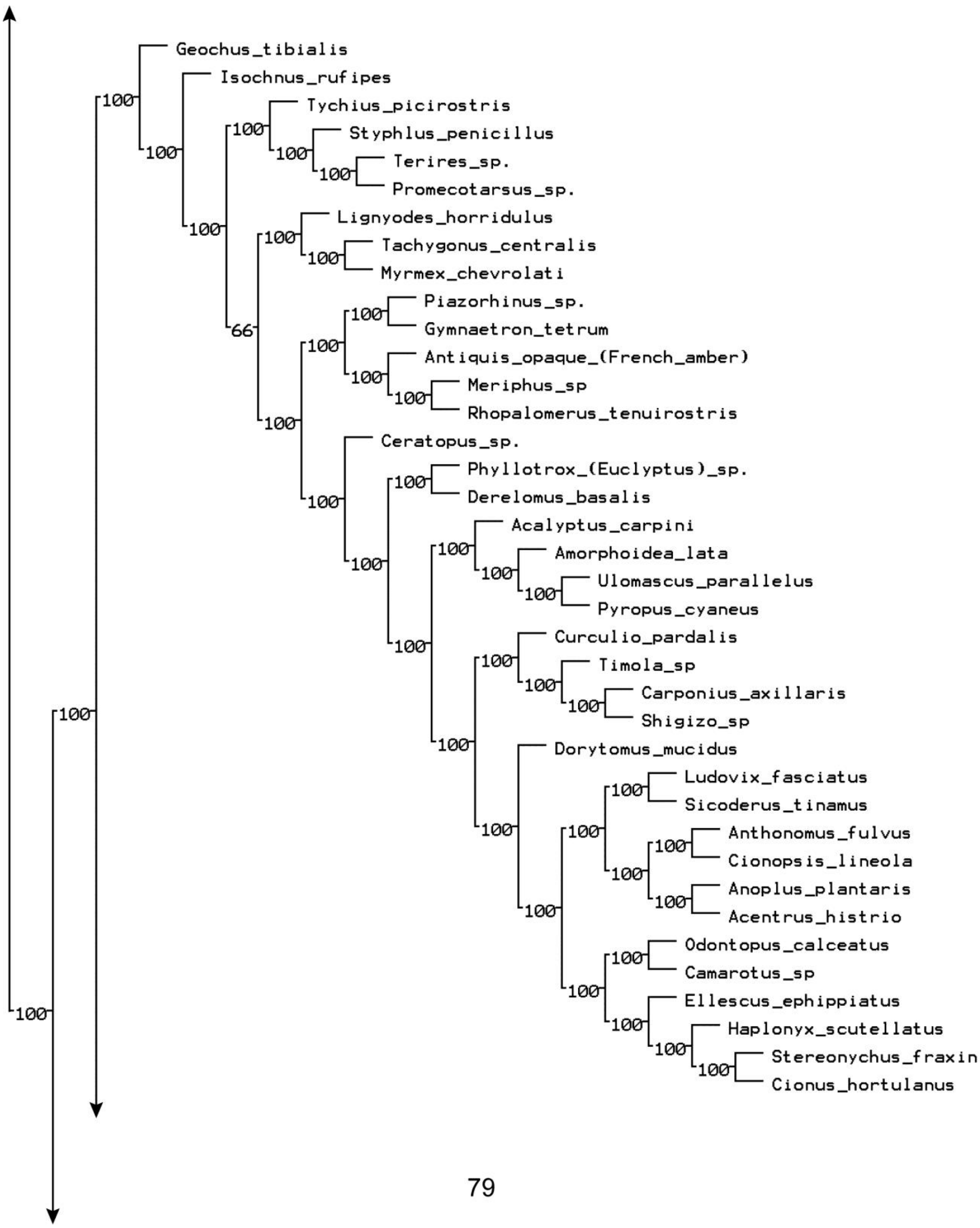
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Gymnaetron_tetrum
Antiquis_opaque_(French_amber)
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Ceratopus_sp.
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Shigizo_sp
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Sicoderus_tinamus
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Cionopsis_lineola
Anoplus_plantaris
Acentrus_histrio
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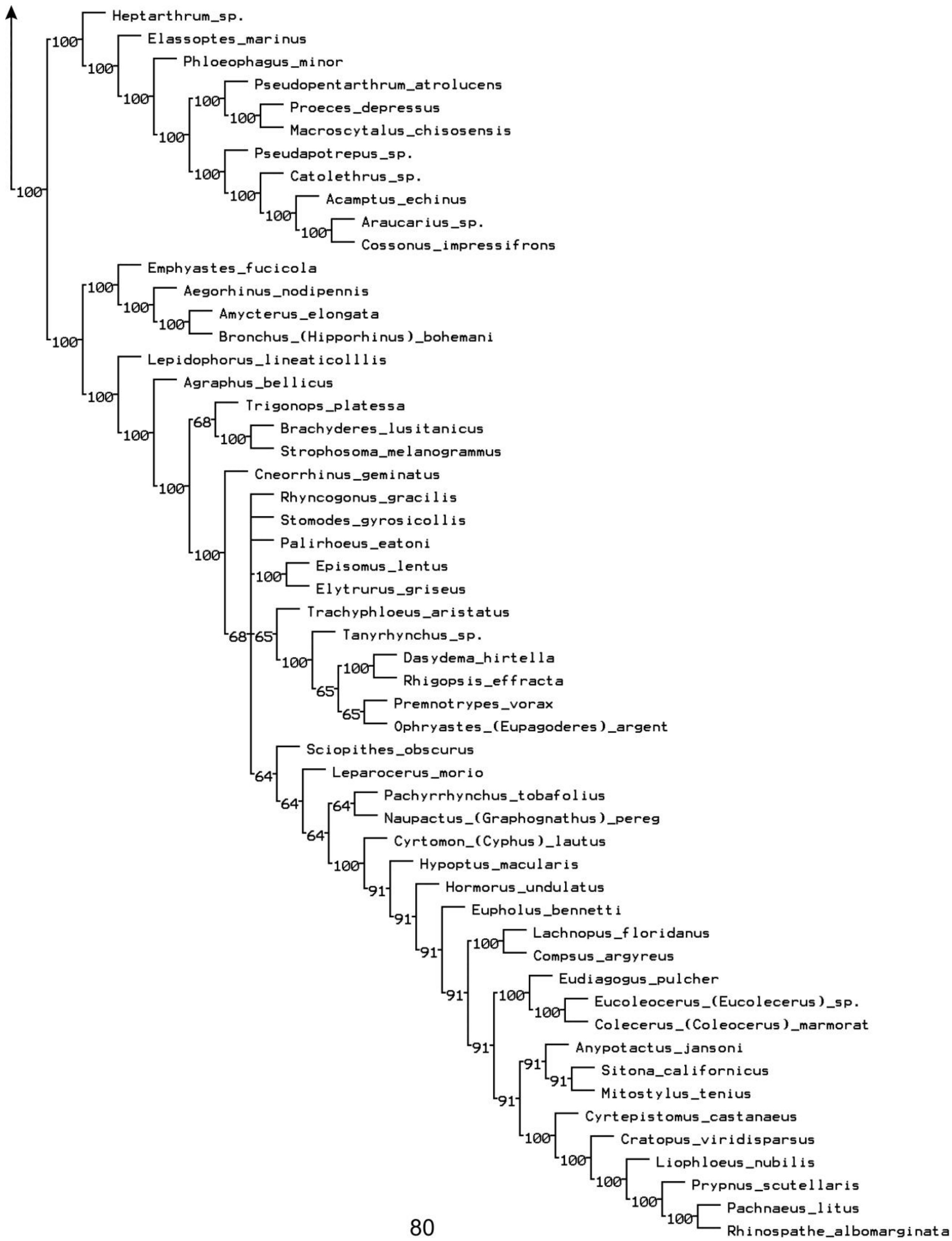
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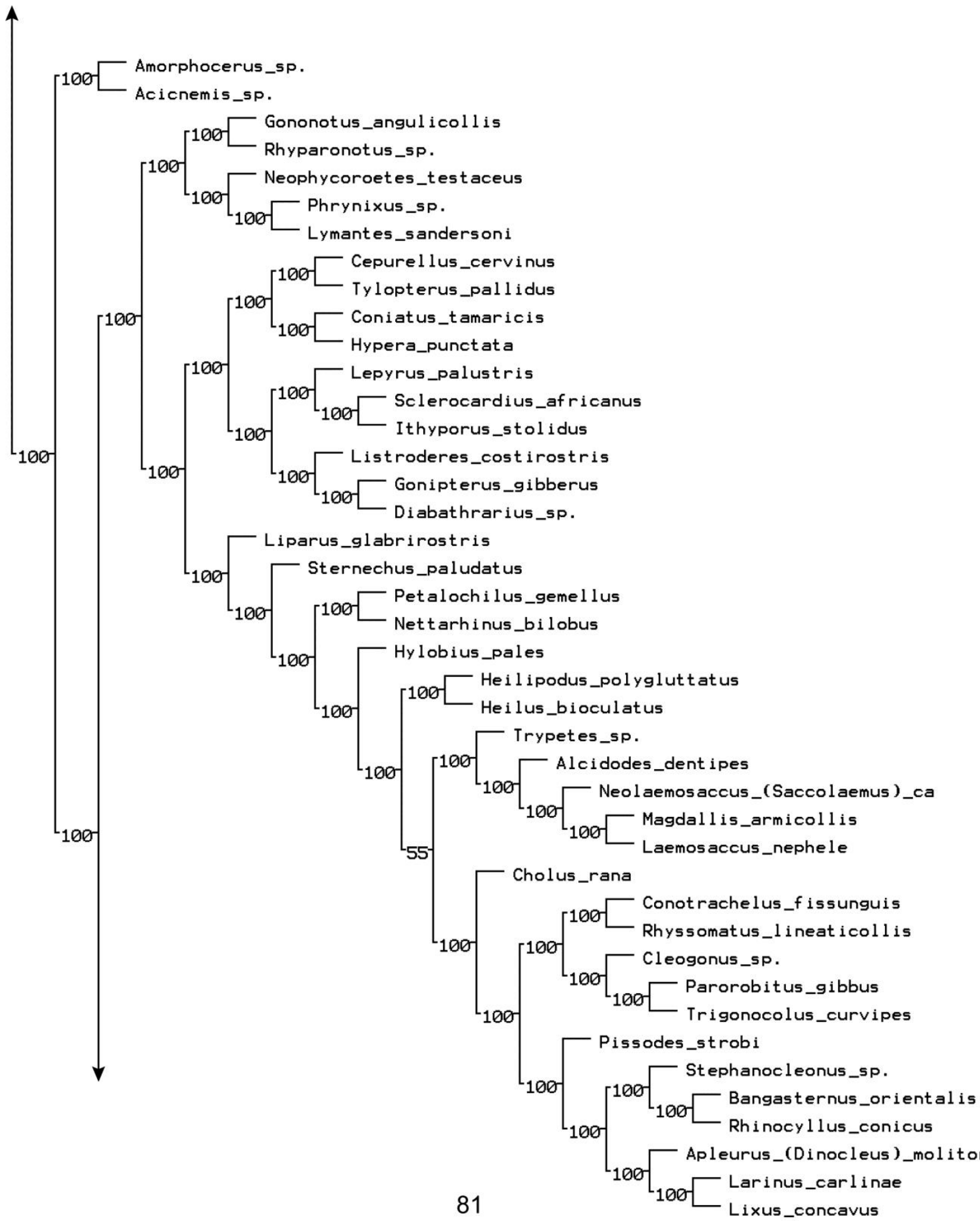
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Pissodes_strobi
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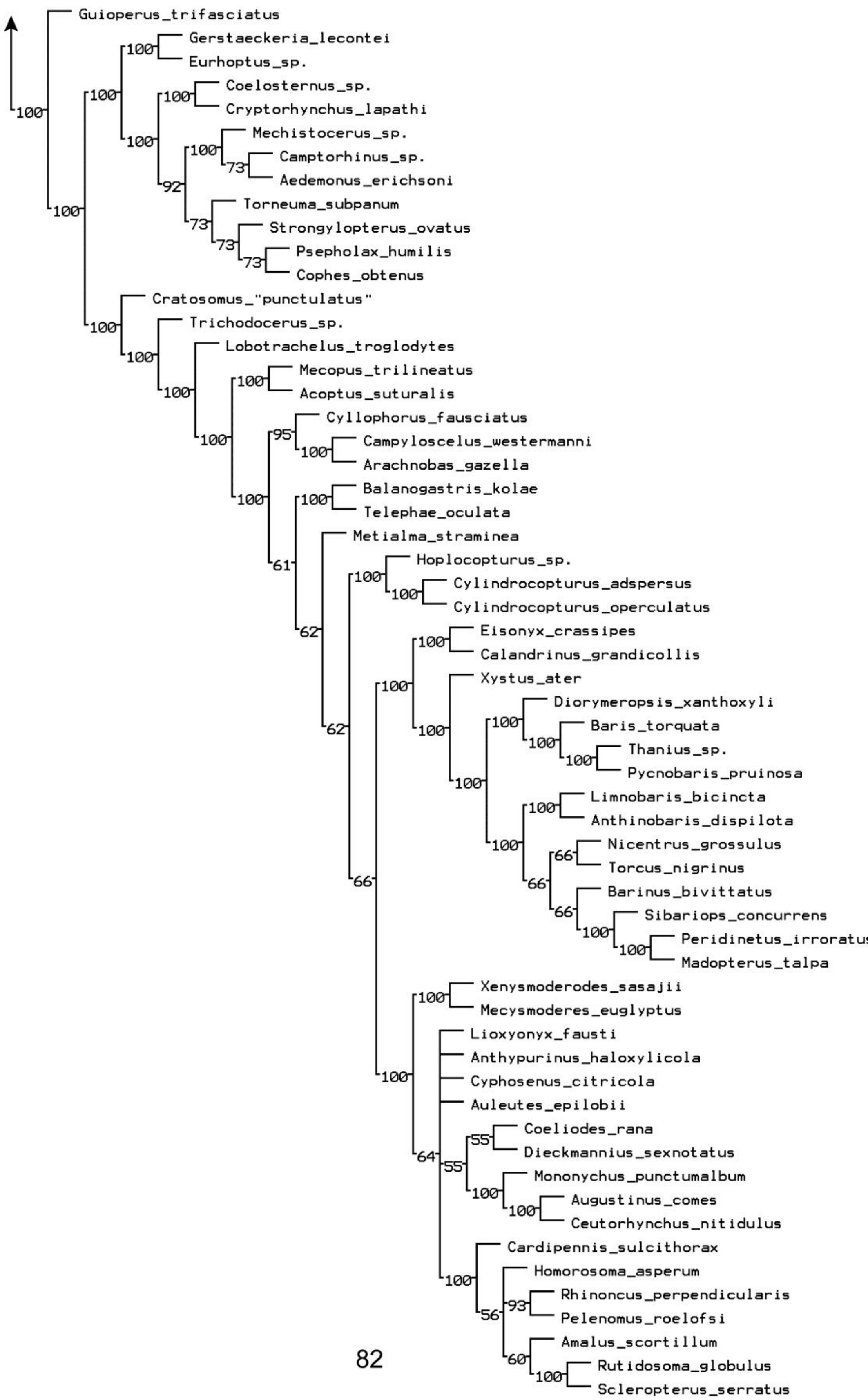
55
81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Anthypurinus_haloxylicola
Cyphosenus_citricola
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Ceutorhynchus_nitidulus
Cardipennis_sulcithorax
Homorosoma_asperum
Rhinoncus_perpendicularis
Pelenomus_roelofsi
Amalus_scortillum
Rutidosoma_globulus
Scleropterus_serratus

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**Appendix A**. Morphological characters and states encoded in this study.

1. body: scales present
    0 absent (only setae)
    1 present

2. antenna: general form
    0 straight
    1 geniculate

3. antennal scape: length
    0 very short, ~equal in length to/<2x length pedicel/funicular articles
    1 short, at least 3x length of pedicel
    2 elongated, >5x length of pedicel

4. antenna: club
    0 absent
    1 present, 3 articles
    2 present, 4 articles
    3 very loose club (primitive curculionoid)
    4 loose club/more defined
    5 present, greater than 4 articles

5. antenna: insertion along rostrum
    0 base
    1 middle
    2 apex

6. rostrum: scrobe
    0 absent
    1 present, not extending beyond antennal insertion
    2 present, extending beyond antennal insertion

7. head: ventral shelf formed by scrobe
    0 absent
    1 present (baridines)

8. head: antenna, club
    0 each article with setae, normal
    1 basal article composing most of club, glabrous; apical articles setose

9. head: antenna, club, antennomere anterior margins
    0 straight (typical type)
    1 convex

10. head: antennal insertion
    0 lateral
    1 dorso-lateral/dorsal
    2 ventral

11. antenna: funicle (including pedicel), # of articles
    0 7
    1 6
    2 5 (Cossoninae)
    3 4 (Cossoninae)
    4 8

12. head: frontal sulci
    0 absent
    1 present (some anthribids)

13. head: frontal shelf (covering antennal insertion)
    0 absent
    1 present, strong (anthribids)
    2 present, weak

14. rostrum: presence
    0 absent
    1 present, short
    2 present, long

15. head: rostrum, dorso-lateral carina
    0 absent
    1 present (Entiminae)

16. head: gula
    0 present
    1 absent (gular sutures fused, continuing with subgenal sutures)
    2 absent (gular suture fused, not continuing with subgenal sutures))
    3 absent, and gular sutures absent
    4 absent posteriorly, only present anteriorly (Dryophthoridae)

17. head: postgula (cervical sclerites)
    0 present, divided (primitive)
    1 absent
    2 present, whole/complete & small/narrow
    3 present, whole/complete & wide

18. head: coronal suture
    0 present, short, ending before eyes
    1 present, long, extending between eyes or beyond
    2 absent

19. head, coronal ridge:
    0 absent
    1 present (Ceutorhynchinae)

20. head: clypeus
    0 present
    1 absent

21. head: labrum
    0 present
    1 absent
    2 partially present, partially fused

22. head: mentum (anterior segment of postmentum)
    0 simple, rectangular (most common)
    1 bilobed (Anthribidae)

23. mandibles: teeth on outer margin
    0 absent
    1 present/exodontous (Rhynchitidae)

24. head: rostrum, medio-longitudinal groove
    0 absent
    1 present (Entiminae)

25. rostrum: medio-longitudinal ridge
    0 absent
    1 present

26. head: rostrum, epistome (dorso-terminal invagination)
    0 absent
    1 present (Entiminae)

27. head: rostrum, subgenal suture length
    0 present, entirely present along length of rostrum
    1 partially present, abbreviated
    2 absent

28. head: rostrum, orientation
    0 anterior (head-rostrum junction ~linear ventrally)
    1 antero-ventral (head-rostrum junction making obtuse angle)
    2 posterior
    3 ventral (head-rostrum junction making v-shape/sub-acute angle)

29. head: size of vertex/frons (area dorsal to rostrum)
    0 large; dorsal rostral margin not flush w/ dorsal head margin; ventral margins flush
    1 small; head rather compressed, dorsal/ventral margins of rostrum ~flush with head margins

30. head: rostrum, shape at apex
    0 rostrum widening
    1 linear, cylindrical

31. head: rostrum, insertion location on head
    0 inserting at base
    1 inserting ~middle (typical condition)

32. head: rostrum, position of occipital suture

0 ventral, complete & separate
1 lateral, complete & separate
2 ventral, incomplete, fused basally
3 ventral, incomplete, fused from base to ~middle
4 ventral, incomplete & separate

33. head: rostrum, subgenal sutures, external presence
0 separate
1 fused at base (head-rostrum junction) only
2 fused for ~first half of rostrum, then diverging
3 absent

34. head: rostrum, pleurostoma (antennal sclerite)
0 restricted laterally
1 extending ventrally, nearly touching (antenna still lateral)
2 extending ventrally and touching (antenna ventral)

35. head: lateral sulcus from occipital foramen
0 absent
1 present (platypodines & scolytines)

36. head: gena, transverse ridges
0 absent
1 present (Rhynchitidae)

37. head: eyes, shape
0 circular
1 longitudinally (vertically) oblong/oval
2 teardrop shape
3 laterally (horizontally) oblong/oval (Apionidae)
4 extremely longitudinally oblong and narrow (crescent-shaped)

38. head: eyes, medial notch
0 absent
1 present (some anthribids)

39. head: eyes, position
0 on head (dorsal to end of genal sutures)
1 on base of rostrum (anterior to end of genal sutures; head constricted before eyes)

40. head: eyes, position
0 lateral
1 anterior
2 latero-ventral, contiguous or nearly touching ventrally

41. head: eyes, convexity
0 strongly convex, bulging
1 flattened

42. head: eyes, size

0 large, with numerous ommatidia (most frequent case)
1 small, with much fewer ommatidia
2 absent
3 enlarged, globose (Rhynchitidae)

43. head: occipital demarkation line
0 absent/indistinct
1 distinct, forming a circular ring/line around posterior part of head

44. head: fovea on frons
0 absent
1 present, small/shallow
2 present, large/deep

45. rostrum: oral fossa, spine between mandible and maxilla
0 absent
1 present
2 present protruding (Attelabidae)

46. head: post-occiput, dorso-lateral expanse (muscle attachment)
0 a single lateral lobe
1 a double lobe
2 a single dorsal lobe

47. head: occiput/post-occiput
0 short, normal
1 elongated (Attelabidae:Apoderinae)

48. head: tentorium, dorsal arms
0 absent
1 present

49. head: tentorium, dorsal bridge
0 absent
1 present, arising from basal part (gular fold)
2 present, arising from anterior arms
3 present, arising at same point of anterior arms
4 bridge arms present but not fusing to form complete bridge

50. head: tentorium, basal part
0 present, fused as 1 part
1 absent (only anterior tentorium present)
2 reduced (anterior arms stil present)
3 present, divided into 2 parts (primitive state)

51. proventriculus:
0 composed of sparse setae/spines not arranged into blades
1 composed of a continuous ring of setal blades (8 rows)
2 composed of a continuous ring of setal blades (16 rows)

52. prothorax: dorsal invagination at procoxal cavity
 0 present and wide, dorsal
 1 absent
 2 present and reduced to short line, dorsal (Apionidae)
 3 present and reduced to line, running anteriorly
 4 present and wide, dorsal, but covered by cuticle
 5 present, reduced to narrow slit
 6 present and reduced to elongate dorsal line (Anthribidae)

53. pronotum: central longitudinal costa/phragma (internal ridge)
 0 absent
 1 present

54. head: post-ocular lobes
 0 absent
 1 present

55. pronotum: dorsal medio-posterior margin
 0 with convex (triangular) protrusion
 1 linear/broadly rounded

56. pronotum: medial longitudinal line
 0 absent
 1 present, distinct

57. pronotum: lateral carina
 0 absent, broadly rounded
 1 partially present, weak, subacute (rounded) edge
 2 strong, acute edge (many anthribids)

58. pronotum: dorso-lateral carina (anthribids)
 0 mostly restricted dorsally, only slightly extending laterally
 1 lateral part extending ventro-laterally, partial
 2 lateral part extending anteriorly (horizontal), partial
 3 lateral part extending anteriorly (horizontal), reaching anterior margin
 4 carinae absent

59. pronotum: dorso-lateral carina, 2nd carina
 0 absent (not differentiated from posterior margin)
 1 present, restricted dorsally
 2 present, extending laterally and slightly anterior (angular laterally)
 3 carinae absent

60. pronotum: shape
 0 narrower than elytra, margins ~parallel/broadly rounded
 1 narrower than elytra only anteriorly, becoming wider posteriorly
 2 ~ as wide as elytra or slightly wider, margins broadly rounded
 3 ~ as wide as elytra, lateral margins parallel (bark beetles)

61. prothorax: constriction at collar

0 absent
1 present (collar present)

62. pronotum: constriction near posterior margin of prothorax
    0 absent
    1 present

63. pronotum: transverse carina near posterior margin
    0 absent
    1 present, immediately adjacent to posterior margin (anthribids)
    2 present, slightly distant from posterior margin (anthribids)

64. prosternum: rostral canal
    0 absent
    1 partially present, not extending beyond procoxae
    2 fully present, extending full length of prosternum

65. prothorax: sternellum
    0 small, not reaching posterior margin (hypomeron forming posterior margin)
    1 large, reaching posterior margin of prosternum

66. prosternum: pleuro-sternal suture
    0 absent
    1 present, complete (continuous from dorsal procoxal suture)
    2 present, incomplete (present only near collar)

67. prothorax: procoxae
    0 at posterior margin (disrupting margin of prosternum)
    1 somewhere in middle of prosternum (not at posterior margin)
    2 in posterior half but not disrupting posterior margin

68. prothorax: procoxae
    0 contiguous (coxal bowls fused)
    1 almost contiguous with just a very narrow separation
    2 completely separated (coxal bowls divergent)

69. prosternum: antero-medial invagination at collar
    0 absent (anterior margin linear)
    1 present, located medially
    2 absent, but anterior margin concave

70. procoxae: coxa-trochanter condyle
    0 not penetrating coxal wall, forming tight cleft from coxal margin (primitive)
    1 penetrating coxal wall, forming condyle visible as circle externally
    2 forming crescent shape (Anthribidae)
    3 not penetrating wall, absent

71. prothorax: internal surface for attachment of part pf proleurotrochantin
    0 short
    1 elongate, developed (bark beetles)

2 slightly lengthened laterally, present apically & absent medially
3 absent

72. prothorax: internal surface for attachment of part pf proleurotrochantin
0 arising from middle of coxal bowl margin
1 arising from anterior margin of coxal bowl margin (brentids)

73. procoxae: shape
0 conical, elongate
1 round, spherical, short

74. prothorax: proendosternite
0 slender
1 expanded apically
2 expanded basally
3 slender, elongated

75. prothorax: proendosternite
0 oriented dorsally
1 oriented posteriorly

76. mesepimeron
0 not ascended
1 ascended

77. mesepisternum: mesal fold
0 with strong central inflection (i.e. mesothoracic collar extended)
1 ~flat (slight vertical inflection line & seemingly no collar)
2 mesal fold reduced/absent but collar present & extended

78. mesepisternum: anterior part at collar
0 not differentiated from posterior part
1 slightly differentiated, with groove for reception of pronotum
2 strongly differentiated from posterior part to fit inside of prothorax

79. mesepisternum: anterior part at collar
0 linear
1 with large anteriorly-directed lobe (platypodines & scolytines)
2 with small anteriorly-directed lobe

80. mesepisternum: anterior part at collar
0 extended (normal)
1 shortened, retracted behind posterior part (Ceutorhynchinae)

81. mesothorax: mesocoxae
0 contiguous (mesosternal process interrupted)
1 completely separated

82. mesosternum: rostral canal
0 absent

1 partially present, only on anterior part of mesosternum
2 fully present, extending full length of mesosternum

83. mesocoxae: intercoxal bridge (internal)
0 coxae fused
1 coxae separate, bridge narrow
2 coxae separate, bridge wide
3 coxae separate, bridge absent

84. mesendosternite: shape
0 fairly linear, slightly bent (~150 degree angle)
1 v-shaped, strongly bent (less than 90 degree angle), often ~60

85. mesendosternite
0 simple
1 arms bifurcate, both arms long and slender
2 arms bifurcate, anterior arm short and wide (a lobe)
3 arms trifurcate (anterior arm shallowly bifurcate)
4 arms bifurcate, short arm lateral and lobe-like (curculionids)

86. mesendosternite:
0 connected to pleuron of mesothorax
1 distal end free

87. mesonotum: axillary cord
0 small, slender
1 enlarged, forming large, discrete lobes
2 enlarged, forming expanded, continuous lobe (Baridinae)

88. mesoscutum: posterior margin (apex)
0 reduced, covered by mesoscutellum
1 enlarged, visible beyond mesoscutellum or nearly so

89. mesonotum: lateral arms of phragma
0 short
1 elongate

90. mesonotum: central phragma
0 enlarged, directed posteriorly
1 relatively small, directed ventrally

91. mesonotum: rim of axillary cord
0 absent
1 present partially
2 present, fully developed, extending entire margin of axillary cord

92. mesoscutellum: height
0 tall, elevated
1 flat/absent or nearly so

93. mesoscutellum: posterior of scutellar stalk
0 rounded, smooth
1 forming acute angle/ridge

94. mesonotum: posterior margin of scutum
0 well-defined, demarcated
1 not well-defined, merging with space of mesoscutellum

95. mesonotum: space between scutum and scutellum
0 wide (much space separating scutum and scutellum)
1 absent or nearly so (scutum touching scutellum)

96. mesonotum: mesoscutum, longitudinal suture
0 present (typical)
1 absent (some Dryophthoridae)

97. mesonotum: posterior of mesoscutum, shape
0 narrow (proportion to scutum)
1 wide

98. metasternum: rostral canal
0 absent
1 present

99. metanotum: lateral lobe
0 absent
1 present (Baridinae)

100. metanotum: posterior margin of metascutum
0 distant from posterior margin of metanotum
1 reaching posterior margin of metanotum

101. metanotum: allocrista
0 posterior margin ill-defined
1 posterior margin well-defined

102. metanotum: allocrista
0 extending full length of scutellar groove
1 abbreviated, ending before middle of scutellar groove (conoderines)

103. metanotum: prescutum
0 posterior margin ~linear (or lateral sclerite forming posterior margin)
1 posterior margin convex (prescutum forming posterior margin)
2 posterior margin ~linear with deep anterior invagination/cleft

104. metanotum: scuto-scutellar ridge, anterior attachment point
0 ridges fusing at connection with anterior margin of scutellar groove
1 ridges fused before reaching anterior margin of scutellar groove
2 ridges not fused, connecting at anterior corners of scutellar groove
3 absent

105. metascutum: postero-medial margin, shape
0 convex, round
1 quadrate
2 concave
3 strongly concave (primitive type)
4 ~linear/straight

106. metanotum: scutellar groove
0 extending full length of metanotum
1 not extending full length (extending ~halfway)
2 not extending full length (nearly reaching posterior margin of metanotum)

107. metanotum: phragma of postnotum
0 slender, small (lobes absent)
1 with large lobes, enlarged
2 enlarged, with a single lobe (platypodines & scolytines)

108. metanotum: phragma of postnotum, orientation
0 directed posteriorly
1 directed ventrally (Baridinae)

109. metanotum: posterior attachment of scuto-scutellar ridge
0 ~ at middle of metanotum
1 laterally displaced

110. metanotum: metascutum, postero-lateral margin
0 acute-subacute
1 round
2 ~linear or only slightly curved laterally
3 quadrate (angled)

111. metanotum: metascutum, posterior margin
0 strongly concave
1 broadly/slightly concave
2 ~linear or only slightly curved laterally
3 linear (transversely)
4 convex

112. metanotum: posterior attachment of metascutum
0 ~ at middle of metanotum
1 laterally displaced
2 closer to scutellar groove

113. metanotum: inflexion point (small internal ridge)
0 present
1 absent

114. metanotum: junction of inflextion point & scuto-scutellar ridge
0 contiguous at posterior margin of metanotum

1 separate

115. metepimeron:
    0 restricted to dorsal side of metepisternum and sclerotized for most of length
    1 restricted to dorsal side and partially sclerotized (basally)
    2 migrated to lateral side of metepisternum, nearly touching metacoxa
    3 enlarged, present along dorsal side of metepisternum (Attelabidae)
    4 very small at postero-dorsal angle
    5 completely fused (absent)

116. metanotum: metascutellum
    0 large, triangular/hemispherical
    1 small, quadrate
    2 nearly absent

117. metanotum: metascutellar line
    0 absent
    1 present

118. metascutum: shape
    0 circular
    1 quadrate
    2 longitudinally elongate (elliptical, ovoid, etc.)

119. metanotum: scutellar groove, longitudinal carina
    0 absent
    1 absent, several transverse ridges present
    2 present

120. metasternum: transverse sulcus (paracoxal) area
    0 present, wide & parallel along entire length
    1 present, narrowing medially
    2 partially present, sulcus not reaching margin
    3 sulcus absent externally but internal carina present
    4 present, narrow mesally becoming very wide laterally (platypodines)
    5 absent

121. metasternum: paracoxal area outside of transverse sulcus
    0 flat, not raised
    1 with raised ridge (derived)
    2 raised ridge reduced to small knob/projection

122. metasternum: median longitudinal sulcus
    0 along entire length of metasternum
    1 abbreviated anteriorly (present along posterior half)
    2 abbreviated posteriorly (present along anterior half)
    3 absent

123. metathorax: lateral phragma of metathorax
    0 slender

1 enlarged, expanded

124. sclerolepidia: types
    0 absent
    1 digitiform (like in Baridinae)
    2 peg-like
    3 setiform, slender

125. metendosternite: stalk, shape
    0 very slender, tall
    1 lateral sides slightly constricted, fairly short
    2 quadrate, fairly short

126. metendosternite: anterior tendons
    0 adjacent to suture
    1 ~along middle
    2 close to furcal arm
    3 on furcal arm

127. metendosternite:
    0 free
    1 fused to sternum

128. metendosternite: hemiductus (lateral arm)
    0 present
    1 absent

129. metendosternite: hemiductus
    0 enlarged, wide
    1 small, slender
    2 absent

130. metendosternite: hemiductus, orientation
    0 directly ventrally (typical)
    1 directed anteriorly (Erirhinidae)

131. metendosternite: furcal arm
    0 simple, narrow
    1 bifurcate
    2 simple, apex expanded/wide

132. metendosternite: furcal arm, orientation
    0 strongly directed posteriorly (arm-stalk angle ~90 deg)
    1 slightly directed posteriorly (~15-45 deg)
    2 directed dorsally (arm-stalk angle ~linear)

133. metendosternite: ventral ramus (forming furcal arm) below sheath
    0 medial section along ventral margin of arm
    1 medial section along median of arm
    2 medial section converging with dorsal ramus (above sheath)

134. metendosternite: lateral cords of stalk
    0 restricted along lateral margins of stalk
    1 converging medially

135. metendosternite: dorsal and ventral components of sheath (ventral view)
    0 open, not produced (primitive)
    1 produced, partially closing to form incomplete tube

136. metendosternite: stalk forming tube
    0 lateral margins folding posteriorly & creating hollow tube at base of stalk
    1 tube absent (lateral margins maybe folding slightly posteriorly)
    2 lateral margins folding posteriorly & forming tube at crux or above
    3 lateral margins folding posteriorly & creating hollow tube near top of stalk
    4 lateral margins folding posteriorly above crux w/o tube
    5 lateral margins folding posteriorly to dorsal margin w/o tube

137. metendosternite: orientation
    0 dorsally
    1 anteriorly

138. tergum: median sclerite 1
    0 subdivided (MS 1 composed of 2 sclerites in total)
    1 each half subdivided (MS 1 composed of 4 sclerites in total)
    2 entire (composed of a single sclerite)

139. tergum: sclerotization
    0 all tergites membranous/lightly sclerotized
    1 tergites partially strongly sclerotized
    2 tergites completely strongly sclerotized (Baridinae)

140. tergum: MS
    0 entire or nearly so (composed of 1 sclerite)
    1 some or all subdivided (composed of 2 sclerites)

141. tergum: laterotergites
    0 absent
    1 small, fragmented
    2 large (Attelabidae)

142. tergum: spiracular sclerites
    0 absent
    1 present, separate from MS
    2 present, fused with MS

143. tergites: spiracular sclerites
    0 absent
    1 present, entire
    2 present, divided

144. tergites: medial groove on tergite 6 or 7
0 absent
1 present

145. abdomen: tergite 7 (male), stridulatory plectra
0 absent
1 present, sparse (with setae)
2 present, dense (with setae)
3 present, with ridges only
4 with setae near lateral margins of tergite
5 plectral ridge along wing-locking patch

146. tergites: lateral locking patch on tergite 7
0 absent
1 present (entimines)

147. tergum: tergite 7, anterior margin
0 smooth, linear (typical)
1 with 2 concave notches (Apionidae)

148. abdomen: tergite 7
0 fairly short, parallel to & separate from sternum
1 elongate, folding ventrally towards sternum (Anthribidae)

149. abdomen: ventrites 1-2:
0 articulating
1 rigid, fused (suture barely visible) (derived)
2 fused, but suture still visible

150. abdomen: ventrite 1, central protrusion
0 triangular, narrowing to acute angle
1 angular, truncated
2 truncated with a central projection
3 triangular, subacute

151. tibia: apical spur/spine formula
0 absent
1 1-2-2
2 2-2-2
3 0-1-1
4 0-2-2
5 0-2-1
6 1-1-1
7 0-1-2

152. tibia: apical spurs
0 present
1 absent

153. tibia: uncus

0 absent
1 present, at outer apical angle
2 present, at middle of apical angle
3 present, at inner apical angle

154. metaleg: coxa, transverse sulcus
0 along entire width of coxa and ending at femoral insertion
1 abbreviated, not meeting femoral insertion
2 absent

155. legs: metatibia, outer apical angle
0 single setal fringe along apical margin
1 single setal fringe before apex, apical margin bare
2 2 setal fringes (along apical margin and just before), separated by bevel
3 distinct setal fringe absent

156. legs: femora, shape
0 narrow, slender
1 enlarged, inflated

157. legs: femoral spine
0 absent
1 present on all femora
2 present only on profemora
3 present only on metafemora
4 present only on mesofemora

158. Legs: femora, dorsal margin
0 smooth
1 w/ longitudinal serrate/crenulate ridge

159. Legs: tibia, dorsal margin
0 smooth
1 w/ longitudinal serrate/crenulate ridge

160. legs: metatibia, outer apical margin
0 linear
1 with lateral flange (in some ceutorhynchines)

161. legs: tibia, outer longitudinal ridge
0 absent
1 present (along full length of tibia)

162. legs: foretibia, inner/ventral margin
0 smooth, devoid of any processes
1 with row of large spines/denticles

163. legs: trochanter
0 triangular, small, femur nearly touching coxa
1 large, femur not touching coxa (only connected to trochanter)

2 greatly elongated (Apionidae)

164. tibia: mucro at inner apical angle
0 absent
1 present

165. legs: tibia, sub-apical setal combs
0 not differentiated, along same distal plane (primitive state)
1 differentiated with proximal (inner angle) and distal combs (outer)

166. legs: foretibia, dense antennal brush on inner apical margin
0 absent
1 present

167. tarsus: tarsomere 1
0 bilobed
1 not divided; narrow, tubular, cylindrical
2 not divided, wide (sub-circular)
3 not divided, conical
4 not divided; enlarged, inflated (much larger than other tarsomeres)

168. legs: tarsomere 1
0 elongated, longer than remaining tarsomeres combined (anthribids)
1 not elongated, relatively short, similar in length to tarsomere 2

169. tarsus: tarsomere 2
0 bilobed/lateral margins extending distally (anthribids)
1 not divided; narrow, tubular, cylindrical
2 not divided, but wide (sub-circular)
3 not divided, conical

170. tarsus: tarsomere 3
0 simple, tubular
1 bilobed

171. legs: tarsomere 3
0 short, lobes small
1 lobes large, elongate and slender
2 lobes large, wide and more round

172. tarsus: pre-tarsal ungues
0 connate
1 narrowly separated
2 widely separated (~170 divergent)

173. tarsus: pre-tarsal ungues
0 simple
1 bifurcate, bifurcation in same vertical plane
2 bifurcate, bifurcation in different vertical planes
3 simple but with subbasal swelling

174. tarsus: tarsomere 4
    0 small, pseudotetramerous case
    1 larger, visible

175. pre-tarsus: empodium
    0 absent/minute
    1 present/enlarged

176. elytra: submarginal fold
    0 absent
    1 present, small
    2 present, enlarged, deep fold

177. elytra: subapical fold
    0 absent
    1 present developed (Baridinae)

178. elytra: apical locking fold (adjacent to elytral suture)
    0 absent
    1 present

179. elytra: erect sensory setae
    0 present
    1 absent

180. elytra: anterior margin
    0 flat
    1 with small transverse groove for reception of pronotum
    2 with large transverse groove for reception of pronotum

181. elytra: apical stridulatory file
    0 absent
    1 present

182. elytra: punctures
    0 absent to minute punctures present; striae absent to shallow
    1 large, noticeable punctures and striae

183. elytra: anterior margin
    0 rounded, latero-anterior margin small and rounded
    1 quadrate, latero-anterior margin produced, large and quadrate

184. elytra: apico-lateral "hook"/flange
    0 absent
    1 present

185. elytra: dorsal surface
    0 relatively linear/gently, broadly and evenly curving (typical)
    1 apical half with declivity (Entiminae)

186. elytra: striae
    0 absent
    1 present

187. hind wing: anal lobe
    0 present, distinctly separated
    1 present, not separate but only enlarged
    2 absent, anal region reduced

188. hind wing venation: Mr - rm connection
    0 Mr diverging from rm (primitive)
    1 Mr smoothly connected to rm (appearing as a single vein)

189. hind wing venation: cu-a
    0 present, complete
    1 present, incomplete/abbreviated
    2 absent

190. hind wing venation: 4A
    0 present
    1 absent

191. hind wing venation: 3A
    0 complete (anal cell present)
    1 incomplete
    2 absent

192. hind wing venation: 3A distal
    0 present, complete to wing margin
    1 present, incomplete (not reaching wing margin)
    2 absent

193. hind wing venation: M1
    0 complete, connecting to Mr (mst absent)
    1 incomplete, mst present and connecting to Mr
    2 incomplete, mst present but not connecting to Mr
    3 M1 absent

194. hind wing venation: a1-a2
    0 present, connecting to 1A2
    1 present, not connecting to 1A2
    2 absent

195. hind wing venation: ? (unknown cross vein)
    0 present
    1 absent

196. hind wing venation: 1A1
    0 present

1 absent

197. hind wing venation: 1A2
0 present
1 absent

198. hind wing venation: Cu2
0 present
1 absent

199. hind wing venation: Cu1
0 complete, reaching wing margin
1 incomplete, af present distally

200. hind wing: radial cell/window
0 present, large (primitive)
1 absent/minute
2 present, small

201. rectum: sclerotized ring
0 present
1 absent (completely membranous)
2 absent, but with an elastic ring (some Entiminae)

202. rectum: sclerotized tube (similar to proventriculus)
0 absent
1 present (anthribids)

203. male terminalia: aedeagus, tegmen
0 complete ring
1 incomplete (ring disrupted)
2 incomplete, jointed laterally

204. male terminalia: aedeagus, tegmen- cap-piece
0 absent
1 deeply bilobed (with 2 parameres [like Baridinae])
2 enlarged and not lobed
3 enlarged and lobed (lobes with setae)
4 cap-piece subdivided into basal & apical sclerites, apical not bilobed (Rhynchitidae)
5 cap-piece subdivided into basal & apical sclerites, apical bilobed

205. male terminalia: aedeagus, manubrium
0 elongate, ~as long as aedeagal struts
1 short, ~0.5x length of aedeagal struts
2 absent

206. male terminalia: manubrium (strut) of tegmen
0 narrow, slender
1 expanded apically (Attelabidae)
2 absent

207. male terminalia: aedeagus, tectum and pedon
  0 similar in size, lateral surfaces of aedeagus membranous
  1 tectum (dorsal plate) small, slender
  2 pedon (ventral plate) enlarged, tectum absent (dorsal surface membranous)
  3 pedon enlarged, tectum absent (dorsal surface sclerotized)
  4 tectum (dorsal plate) largely absent, reduced to a bridge

208. male terminalia: sternite 8
  0 entire
  1 divided (forming hemisternites; many curculionids)
  2 absent/membranous

209. male terminalia: sternite 9, basal part (w/ spiculum)
  0 present, large, expanded
  1 present, slender, transverse
  2 absent

210. male terminalia: sternite 9, apical part
  0 present (separate from basal part), subdivided
  1 absent (membranous)
  2 present but reduced, forming short, slender sclerite (Brentidae)
  3 present (separate from basal part), a single large sclerite
  4 present & subdivided but fused to basal part (some entimines)

211. male terminalia: aedeagal struts
  0 separate from median lobe/aedeagal body
  1 fused with aedeagal body

212. male terminalia: aedeagal struts
  0 divided basally, separate parts fusing apically
  1 divided until median then fusing at apical half
  2 fused along entire length

213. male terminalia: aedeagal struts, width
  0 fused, forming elongate sclerite
  1 divided, wide
  2 divided, narrow/slender

214. male terminalia: tergite 8, anterior margin
  0 concave or with cleft
  1 linear or convex
  2 tergite divided (anthribids)

215. male terminalia: tergite 8
  0 entirely sclerotized
  1 sclerotized along margins & membranous medially (Anthribidae)

216. male terminalia: tergite 8, form
  0 lateral margins converging ventrally (tergite nearly tubular)

1 tergite 8 ~flat or slightly curved

217. male genitalia: tergite 8, apex
0 complete, round
1 forming a pair of elongate lobes (some anthribids)
2 only slightly lobed

218. male terminalia: spiculum gastrale
0 "2 present" (Nemonychidae)
1 singular (most typical type)
2 absent

219. male terminalia: spiculum gastrale, form
0 fused (typical)
1 separate at base
2 absent

220. female terminalia: stylus (gonostylus)
0 enlarged, modified with serrations
1 small, minute with apical setae
2 enlarged, sclerotized

221. female terminalia: stylus
0 present
1 absent

222. female terminalia: coxite (gonocoxa)
0 complete
1 subdivided longitudinally
2 absent
3 subdivided horizontally, medially

223. female terminalia: coxite, baculus (longitudinal stripe)
0 present, elongated and forming struts
1 present, short, not extending beyond coxite
2 absent

224. female terminalia: coxite (gonocoxa)
0 greatly elongated, narrow
1 short, narrow
2 absent
3 short, wide & flattened (some entimines)

225. female terminalia: ovipositor
0 telescoping
1 absent, not telescoping

226. female terminalia: sternite 8, apex
0 entire
1 bilobed and open (Baridinae)

2 bilobed but closed
3 absent

227. female terminalia: sternite 8, struts
0 fused (most common type)
1 separate
2 struts absent
3 fused only at anterior apex (Dryophthoridae)

228. female terminalia: tergite 8
0 posterior margin smooth
1 posterior margin w/ large teeth (Brentidae)

229. pronotum, postero-lateral margin:
0 with broad medial lobe/projection (belids)
1 lobe/projection absent, margin smooth
2 with small medial lobe/projection/knob (anthribids)
3 dorsal part of pronotum forming broad cleft

230. pronotum, postero-dorsal margin:
0 receding anteriorly (belids)
1 not receding, remaining flush at posterior margin

231. pronotum: posterior margin
0 thin, not differentiated
1 slightly thick, widened (particularly laterally) for reception of mesothorax
2 very thick, widened (derived)

232. mesepimeron:
0 short, dorsal margin below that of metepisternum (basal weevils)/reduced in size
1 tall, dorsal margin ~flush with or taller than that of metepisternum
2 tall but very slender, small (entimines)

233. mesepimeron: form
0 flush with metepisternum, not differentiated
1 slightly projecting outwards/slightly differentiated
2 strongly projecting outwards/strongly differentiated, forming dorsal cleft

234. metepisternum, antero-dorsal lobe:
0 absent, antero-dorsal margin linear (basal weevils)
1 present
2 absent, but margin broadly curved and pointed

235. metepisternum: presence
0 separate from metasternum
1 fused to metasternum, undifferentiated (entimines, cyclomines)

236. ventrites, pre-lateral emargination:
0 absent/not differentiated laterally
1 present (belids), slightly differentiated

2 strongly differentiated, distinctly different from sternite (higher weevils)

237. tarsus: ventral setal tufts (particularly on tarsomeres 1-2)
    0 distinctly divided along midline
    1 not divided (higher weevils)

238. hing wing venation: Rr
    0 present
    1 absent

239. hind wing venation: R3
    0 present
    1 absent

240. hind wing venation: rms
    0 present
    1 absent

241. hind wing venation: 2rs
    0 present
    1 absent

242. hind wing venation: 1rs
    0 present
    1 absent

243. hind wing venation: pst
    0 present
    1 absent

244. hind wing venation: rsc
    0 separate from mst, extending slightly towards wing apex
    1 fusing with mst (higher weevils)
    2 absent

245. hind wing venation: rf
    0 present
    1 absent

246. hind wing venation: rm
    0 present
    1 absent/very faint

247. hind wing venation: rm, dorsal connection
    0 connecting to radial cell
    1 connecting to Rr (anthribids)

248. hind wing venation: wing proportions
    0 basal venation (until mcu) exceding > half of wing length
    1 basal venation (until mcu) ending at ~ middle of wing length

2 basal venation (until mcu) ending < half of wing length

249. elytra: notch at antero-lateral margin
0 absent
1 present (derived)

250. elytra: ball and notch at antero-mesal margin of suture
0 absent
1 present (derived)

251. antenna: funicular article 2 (flagellomere 3)
0 longer than pedicel
1 similar in length to pedicel
2 ~3x longer than pedicel

252. ventrites:
0 all similar in length
1 3-5 shorter than 1 &/or 2 (higher weevils)
2 2-5 shorter than 1 (which is long)

253. abdomen: ventrite 1, central protrusion
0 small
1 enlarged (higher weevils)

254. pronotum: medio-longitudinal depression/groove
0 absent
1 present, complete
2 partially present, abbreviated to posterior margin

255. mesonotum: posterior margin
0 linear
1 lobed/rounded/broadly convex
2 with acute/subacute projecting margin

256. metanotum: allocrista (margins of scutellar groove)
0 ~parallel
1 slightly diverging anteriorly
2 strongly diverging anteriorly (scutellar groove often wide in this case)

257. metasternum: inter-metacoxal area (covered by ant. abd. projection)
0 narrow, not strongly differentiated from rest of metathorax (primitive)
1 wide, strongly differentiated from rest of metathorax

258. female terminalia: tergite 9
0 sclerotized (visible as a pair)
1 membranous/indiscernible

259. abdomen: sternites 1 & 2
0 incompletely fused, 1 somewhat lobed/not flush with 2
1 incompletely fused, 1 flush with 2

2 completed fused

260. abdomen: tergite 1
0 whole/entire
1 partially subdivided horizontally into anterior and posterior parts
2 completely subdivided horizontally

261. abdomen: tergite 2
0 whole/entire
1 partially subdivided horizontally into anterior and posterior parts
2 completely subdivided horizontally

262. metanotum: metascutum
0 entire
1 subdivided along lateral margin near 1Ax

263. metanotum: metascutum posterior to 1Ax
0 entire, anterior part falciform
1 partially subdivided
2 completely subdivided

264. metathorax: wing locking patch (dorsal part of metepimeron)
0 membranous/weakly sclerotized
1 strongly scerlotized

265. metathorax: wing locking patch (dorsal part of metepimeron)
0 patch separated from metepimeron
1 patch fused with metepimeron (higher weevils)

266. metathorax: small sclerite dorsal to metepimeron locking patch
0 absent/membranous
1 present/sclerotized

267. female terminalia: tergite 8
0 incomplete/divided
1 entire with anterior portion concave and membranous
2 entire with whole tergite sclerotized
3 divided apically (dryophthorids)

268. female terminalia: lobes of spermatheca
0 4
1 3
2 two
3 1 (linear/curved)

269. female terminalia: shape of spermatheca
0 falciform (higher weevils)
1 linear (curved)
2 3-furcate (belids)

270. female terminalia: spermatheca, ramus (connecting to sperm. gland)
    0 not produced into lobe
    1 produced into lobe

271. female terminalia: spermatheca, collum (connecting to sperm. duct)
    0 not produced into lobe
    1 produced into lobe

272. female terminalia: ventrite 5, internal apodeme pair
    0 absent
    1 present

273. mouthparts: postmentum, shape
    0 enlarged and bilobed (anthribids)
    1 narrow, elongate

274. mouthparts: labium, prementum-palpus ratio
    0 palps long, prementum small (primitive)
    1 palps relatively short, prementum moderately large

275. mouthparts: prementum, size
    0 small-medium
    1 enlarged, inflated/globose
    2 enlarged, flattened (bearing wing-like extensions) (nemonychids)

276. mouthparts: prementum
    0 entirely distal of postmentum
    1 nested within apex of postmentum (apex of postmentum wrapping laterally)

277. mouthparts: labial palps
    0 elongated
    1 moderately long (typical)
    2 small, very short
    3 absent

278. mouthparts: labium, palpus insertion
    0 subapically
    1 apically

279. mouthparts: labium, prementum bearing paraglossae
    0 present (primitive)
    1 absent

280. mouthparts: labium, setae on prementum
    0 restricted along lateral margins
    1 restricted to apical margin, ~in linear row
    2 setae in no distinct pattern, scattered

281. mouthparts: labium, ligula
    0 sclerotized (belids)

1 membranous

282. mouthparts: labium, palpal segment #
0 3
1 2
2 1

283. mouthparts: maxilla, palpal segment #
0 4
1 3
2 two

284. mouthparts: maxilla, stipes
0 vertically flush with palpus
1 laterally projecting

285. mouthparts: maxilla, sensory organs on apical palpal segment
0 absent
1 arranged vertically
2 arranged laterally
3 arranged circularly

286. mouthparts: maxilla, setae on lacinia & galea
0 large tooth-like, falciform setae present
1 such setae absent

287. mouthparts: maxilla, setae on lacinia & galea
0 medium-sized setae present
1 such setae absent

288. mouthparts: maxilla, setae on lacinia & galea
0 slender, elongate setae present
1 such setae absent

289. mouthparts: maxilla, elongate setae at apico-lateral margin of palpiger
0 present
1 absent

290. mouthparts: maxilla, lacinia & galea
0 separate (primitive)
1 fused

291. mouthparts: maxilla, basal palpomere
0 small (primitive)
1 large
2 large with extended digitiform projection, as long as palpus

292. mouthparts: maxilla, lacinia
0 tuft of elongate, slender setae at latero-basal margin
1 slender setae absent along this margin

293. mouthparts: maxilla, palpus
0 palpal segments short, compacted
1 palpal segments long, not compacted

294. mouthparts: maxilla, palpus
0 3rd apical segment proportionally slightly smaller than 1st & 2nd
1 3rd segment tiny, much smaller than 1st & 2nd
2 3rd segment not smaller, similar in size or larger

295. mouthparts: mandible, preartis (socket)
0 medio-basal
1 latero-basal, lateral margin linear
2 strongly latero-basal, lateral margin lobed
3 mesal (along inner margin)

296. mouthparts: mandible, postartis (ball)
0 medio-basal
1 latero-basal

297. mouthparts: mandible, shape
0 slender, spiniform
1 wide, digitiform
2 wide, block-shaped

298. mouthparts: mandible, incisor direction/shape
0 linear, straight
1 curved/falciform
2 block-shaped

299. mouthparts: mandible, diciduous cusp
0 absent
1 present

300. mouthparts: mandible, incisor #
0 1
1 2
2 3
3 4

301. mouthparts: mandible, mola
0 reduced/absent
1 large

302. mouthparts: mandible, incisor proportions
0 1st incisor largest
1 2nd incisor largest
2 3rd incisor largest

303. mouthparts: mandible, setae

0 absent
1 present, restricted to tuft at lateral margin
2 present, scattered all over surface

304. mouthparts: mandible, outer margin
0 ~flush, smooth, linear/curved
1 with notch/concavity just above articulation

305. mouthparts: mandible, longitudinal groove w/ setae near outer margin
0 absent
1 present

306. hind wing: antero-basal margin of Sc
0 swollen, enlarged
1 not swollen, narrow

307. hind wing: antero-medial margin of 3Ax
0 with small anterior acute projection
1 without projection, anterior margin smooth

308. hind wing: MP and 3Ax
0 largely separated
1 mostly fused

309. hind wing: MP and MB
0 largely separated
1 mostly fused

310. hind wing: slit just dorsal to base of Cu
0 present, developed, crescent-shaped
1 absent, reduced/shortened

311. hind wing: anterior of 1Ax
0 lateral margins smooth
1 with distinct knob; outer margin with small notch

312. hind wing: antero-subbasal lobe on C
0 absent, anterior margin smooth
1 present

313. elytra: scutellary striole
0 absent
1 present

314. tergites: lateral paired pits
0 absent
1 present

315. proventriculus: form
0 forming cylinder, diameter subequal along length

1 abruptly expanding at crop

316. metanotum: metanotum and allocrista
    0 allocrista extending beyond intersection with metanotum
    1 allocrista extending until (& not surpassing) intersection with metanotum

317. metacoxa: internal anterior lobe
    0 present, small lobe (primitive)
    1 absent, anterior margin broadly incurved
    2 present, broad lobe

318. head: medio-longitudinal interocular sulcus (disjunct from coronal suture)
    0 absent
    1 present, well-developed & distinct, forming strong phragma
    2 partially present, weak

319. procoxa: propleurotrochantin, shape
    0 short
    1 elongate

320. male terminalia, aedeagus: dorso-basal strut structure
    0 composed of dorsal & ventral components fusing laterally
    1 composed of dorsal & ventral components fusing dorsally
    2 composed of dorsal & ventral components fusing dorsally, tectum reduced to bridge
    3 struts lateral (composed of dosal pedon part)
    4 dorsal strut pair absent

321. male terminalia, aedeagus: lateral division of pedon
    0 absent
    1 present (dryophthorids)

322. male terminalia, aedeagus: ventro-basal strut structure
    0 ventral strut pair absent
    1 struts lateral
    2 struts ventral

323. antennae: joint between scape and pedicel
    0 orthocerous, socket on scape located apically
    1 geniculate, socket on scape located laterally

324. head, rostrum: pleurostomal sulcus
    0 present
    1 absent

325. head, rostrum: subgenal sulci, internal apodemes
    0 present
    1 absent

326. elytra: lateral submarginal carina
    0 absent

1 present

**Appendix B**. Morphological character matrix of 577 taxa and 282 characters.

```
Characters 0 - 32
                                               0    5    10   15   20   25   30
                                               |    |    |    |    |    |    |
Cucujus clavipes                               000000040000000012000000000001--10
Orsodacne atra childreni (Orsodacnidae)        000000000100000012000000000001--10
Fidia viticida (Chrysomelidae)                 000000000100000011000000000001--10
Cimberis sp.                                   0000200000000200000101000000010110
Nannomacer germaini                            0003200000000200020101000000010110
Mecomacer scambus                              0003200000000200020101000000010110
Rhynchitomacerinus kuscheli                    0003200000000200020101000000010110
Nemonyx lepturoides                            0003200001000100000101000000010110
Doydirhynchus austriacus                       0003000001000200000101000000010110
Lecontellus byturoides                         0003100001000200000101000000010110
Arra similis (Spanish amber)                   0003200000000200?0101000000010100
indet 5 anthribid (Yixian 2005126)             00042??0000??2012?0??000000011101
Trigonorhinus sp.                              000320000000110000010100002011113
Anthribus nebulosus                            000421000100110300010100002011113
Epicerastes sp.                                100321000100110300010100002011113
Apolecta samarana                              000321000100110300010100002011113
Gynandrocerus sp.                              000421000110110300010100102011113
Phaenithon semigriseum                         000420000000110300010100002011113
Basitropis sp.                                 000421000100110300010100102011113
Strabus bimaculatus                            000421000100110300010100002011113
Corrhecerus sp                                 000421000100110301010100002011113
Straboscopus tessellatus                       000421000100110301010100102011113
Euparius marmoreus                             000420000000110300010100002111113
Discotenes nigrotuberculata                    000420000000110300010100002111113
Ischnocerus infuscatus                         000421000100110300010100101010111
Dendropemon sp.                                000221000110110300010100002011113
Eucorynus crassicornis                         000221000110110300010100002011113
Gymnognathus sp.                               000420000000110300010100002111113
Dinema filicornis                              000300000101110300010100002111113
Neseonos brunneus                              000420000101110301010100002111113
Mauia subnotata                                000321000100110300010100002111113
Illis anna                                     000321000100110300010100002110113
Mecocerus sp.                                  000321000100120301010100101010111
Acanthothorax basalis                          000321000100120301010100101010111
Phloeophilus sulcifrons                        000321000100120301010100101010111
Mycetis marginicollis                          000311000100120301010100101010111
Ormiscus sp.                                   000420000000110300010100002111113
Ozotomerus bipunctatus                         000420000100110300010100102111113
Piesocorynus sellatus                          000220000001011030001010000211111 3
Brachycorynus distentus                        000421000100110300010100002011113
Goniocloeus sp.                                000420000000110301010100002011113
Platyrhinus resinosus                          000421000101110301010100001010111
Phoenicobiella chamaeropis                     000420000001020301010100002010113
Toxonotus fascicularis                         000421000100210301010100102010113
Phloeobius pallipes                            000420000101210301010100102110113
Platystomos wallacei                           000420000100210301010100102110113
Ptychoderes sp.                                000420000100221301010100112010113
Phloeotragus polyopras                         000320000100020301010100110010112
Cerambyrhynchus schoenherri                    000320000100010300010100102010113
Rhinotropis superciliaris                      000321000101110301010100002010113
Sintor quadrilineatus                          000322000101220300010100000010113
Allandrus bifasciatus                          000420000000120301010100102010113
Stenocerus sp.                                 000321000100121300010100100010111
Plintheria plintheroides                       000421000100120300010100001110112
Trigonorhinus sticticus                        000420000000220300010100002110113
Tropideres fasciatus                           000420000001120301010100102110113
Acorynus pallipes                              000321000101121301010100100110110
Cedus guttatus                                 000321000101111301010100101110111
```

| | |
|---|---|
| Xenocerus ancyra | 00032100010121130101010011211O113 |
| Xylinada rugicollis | 00042000000121130001010010211O113 |
| Stiboderes westermanni | 000321000100211300010100111110110 |
| Exechesops bakeri | 000300000100110301010100002111113 |
| Holostilpna sp. | 000400000100010300010100002111113 |
| Choragus sayi | 000301000100010300010100002111113 |
| Euxenus jordani | 000300000101010300010100002111113 |
| Araecerus levipennis | 000400000100010300010100002111113 |
| Acaromimus americanus | 000400000101010300010100002111113 |
| Misthosima sp. | 000300000101010300010100002111113 |
| Cisanthribus sp. | 000400000101010300010100002111113 |
| Notioxenus ater | 000401000100010300010100002111113 |
| Urodon rufipes | 000421000101210300010100002111113 |
| Rhinotia sp. | 000010000000002000001100000011010 |
| Belus semipunctatus | 000010000000002000001100000001012 |
| Homalocerus lyciformis | 000000000000002000201100000011011 |
| Pachyura australis | 000020000000002000201100000011010 |
| Dicordylus marmoratus | 000010000000002000001100000011012 |
| Daohugou belid sp. | 000010000000000200???110?000?011012 |
| Montsecbelus solutus | 0003200000000020???0???0000?0110?? |
| Car sp. | 002300000200020102011000000011102 |
| Car condensatus | 001000000200020102011010000011102 |
| Caenominurus topali | 001300000000020102011000000011102 |
| Albicar contriti (Spanish amber) | 001300000000020102011000000011101 |
| Chilecar pilgerodendri | 001300000000020102011000000011102 |
| Carodes revelatus | 001000000000020102011000000011102 |
| Baissorhynchus tarsalis | 002410000000020102011000000011101 |
| Paleocar princeps | 00241000000002010201?000000111101 |
| Baissacar passarius | 00241000000002010201?000000111101 |
| Cretonanophyes longirostris | 001410000000020102011000000011101 |
| Cretonanophyes punctatus | 001410000000020102011000000011101 |
| C. punctatus (Yixian 2007105 1/2) | 00?31??0000??2012?0??000000010101 |
| C. punctatus (Yixian 2006103) | 00?41??0000??2012?0??000000010101 |
| C. punctatus (Yixian 2005115) | 00?41??0000??2012?0??000000010101 |
| C. punctatus (Yixian 2010158) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2006101) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2005113) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2005114) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2005109) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2005112) | 00?41??0000??2012?0??000000010101 |
| C. zherikhini (Yixian 2005103) | 00?41??0000??2012?0??000000010101 |
| Cretonanophyes asiaticus (sp1) | 00141000000002010 20??000000011101 |
| Cretonanophyes neocomicus (sp2) | 001410000000020102011000000011101 |
| Jarzembowskia edmundi | 0013000000000201???11?00000011101 |
| Baissacarodes sibiricus | 00241000000000201020??000000011101 |
| Emanrhynchus lebedevi | 00241000000000201020??000000011101 |
| Gobicar ponomarenkoi | 00141000000000201020??000000011101 |
| Gobicar ulugeiensis | 00141000000000201020??000000011101 |
| Mesophyletis calhouni | 0023100000000020???0110100 0?0111?? |
| Hispanocar kseniae | 0014100000000020???0???0000?0111?? |
| Martinsnetoa dubia | 00140000?00020???0???0000?0111?? |
| Cretocar luzzii | 00140000020002 0???01100000?0111?? |
| Montsecanomalus zherikhini | 0003100000000020???0???0000?0111?? |
| Zigras cornus | 0023100002000201?20110000 0?011101 |
| Zigras nudicornus | 0023100000000201?201100000?011101 |
| Scabridus implexus | 0023110002000201?201100000?011101 |
| Scabridus zigrasi | 0023100002000201?201100000?011101 |
| Anchineus dolichobothris | 0024120000000201??0??01000001110? |
| Caridae 1 | 002?100000000201?201100000?0111?? |
| Caridae 2 | 0024100000000201?201100000?1111?? |
| Caridae 3 | 0023100002000201?201100000?011101 |
| Preclarusbelus vanini | 00?4000002000020???0????000?0111?? |

| | |
|---|---|
| Arariperhinus monnei | 00?41000020002O???0???0000?0111?? |
| Gratshevbelus erici | 00?30000020002O???0???0000?0111?? |
| Proterhinus sp. | 000310000000010300011000001011111 |
| Rhopalotria bicolor | 001300000000020100011000000011112 |
| Parallocorynus bicolor | 001300000000020100011000000011112 |
| Baltocar succinicus | 000400000000201??01101000?0111?? |
| Haplorhynchites aeneus | 000310000000020100011010010010111 |
| Involvulus hirtus | 000310000000020100011110010010111 |
| Merhynchites bicolor | 000320000000020100011010010010111 |
| Eugnamptus punctatus | 000310000000020100011010010010112 |
| Auletobius cassandrae | 000300000000020100011010010010012 |
| Minurus testaceus | 000310000000020120012010010011111 |
| Pseudauletes sp. | 000300000000020120012010010010012 |
| Byctiscus populi | 000310000100020120012010010010111 |
| Listrobytiscus corvinus coeruleipennis | 000310000100020120012010010010112 |
| Deporaus glastinus | 000300000000020100011010000010012 |
| Pterocolus ovatus | 000310000000020100011010000011112 |
| Homeolabus analis | 000310000100020120012000000010112 |
| Attelabus nigripes | 000310000100020120012000000010112 |
| Omolabus conicollis | 000310000100020120012000010110112 |
| Euscelus dentipes | 000310000100020120011000000010112 |
| Henicolabus octospilotus | 000300000100020120011000000010112 |
| Lamprolabus sandacanus | 000310000100020120012000010110112 |
| Euops quadrifasciculatus | 000400000100020122011000000010112 |
| Pilolabus viridans | 000410000100020122011000000010112 |
| Apoderus sp. | 000410000100010121011000000010112 |
| Parapoderus flavoebenus | 000410000100010121011000000010112 |
| Clitostylus badeni | 000410000100010121011000000010112 |
| Holapoderus hystrix | 000410000100010121011000000010112 |
| Paroplapoderus pardalis | 000410000100010121011000000010112 |
| Cynotrachelus roelofsi | 000420000100010121011000000010112 |
| Trachelophorus giraffa | 000420000100010121011000000010112 |
| Ithycerus novemboracensis | 000210000000020102011000000010112 |
| Brentus anchorago | 001320000000020102011000001010122 |
| Arrhenodes minutus | 001310000000020102011000001010122 |
| Henarrhenodes macgregori | 000311000000020102011000001010122 |
| Baryrrhynchus schroderi | 000311000000020102011000001010122 |
| Amorphocephala imitator | 000320000000220102011000001010122 |
| Antliarhinites zamiae | 001320000000220102011000001010122 |
| Cylas formicarius elegantulus | 000122000000020102011000001010122 |
| Oncodemerus sennai | 000310000000220102011000001010122 |
| Stereodermus latirostris | 000310000000020102011000001010122 |
| Cerobates sexsulcatus | 000310000000020102011000001010122 |
| Taphroderopsis oscillator | 000310000000020102011000001010122 |
| Paratrachelizus uncimanus | 000310000000020102011000001010122 |
| Miolispa robusta | 000310000000020102011000001010122 |
| Nemocephalus guatemalensis | 000320000000020102011000001010122 |
| Diuris shelfordi | 000320000000020102011000001010122 |
| Ithystenus hollandiae | 000320000000020102011000001010122 |
| Schizotrachelus bakeri | 000310000000020102011000001010122 |
| Hormocerus scrobicollis | 000310000000020102011000001010122 |
| Ulocerus sp. | 101121000000020102011000001010111 |
| Aporhina sp. | 000311000000020100011000000011111 |
| Apion longirostre | 101101000000020222011000001011122 |
| Sayapion arizona | 101112000000020222011000001011122 |
| Perapion punctinasum | 101101000000020222011000001011122 |
| Phrissotrichum tubiferum | 101102000000020222011000001011122 |
| Alocentron attenuatum | 101101000000020222011000001011122 |
| Aspidapion radiolus | 101102000000020222011000001011122 |
| Ceratapion basicorne | 101101000000020222011000001011122 |
| Omphalapion hookeri | 100102000000020222011000001011122 |
| Cybebus dimidiatus | 101102000000020222011000001011122 |

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| Exapion ulicis | 10110100000000202220110000001111122 |
| Ixapion herculanum | 10010100000000202220110000001011122 |
| Kalcapion flavofemoratum | 10110100000000202220110000001011122 |
| Melanapion minimum | 10010100000000202220110000001011122 |
| Malvapion malvae | 10110100000000202220110000001011122 |
| Rhopalapion longirostre | 10010100000000202220110000001011122 |
| Noterapion meorrhynchum | 10111100000000202220110000001011122 |
| Eutrichapion alakanum | 10110100000000202220110000001011122 |
| Capapion seniculus | 10010100000000202220110000001011122 |
| Stenopterapion tenue | 10010100000000202220110000001011122 |
| Trichapion gracilirostre | 10110200000000202220110000001011122 |
| Chrysapion auctum | 10110100000000202220110000001011122 |
| Protapion apricans | 10011200000000202220110000001011122 |
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| Nanophyes canadensis | 00211200002002020201100000001111112 |
| Dieckmanniellus nitidulus | 00211200002002020201100000001111112 |
| Corimalia tamarisei | 00211200002002020201100000001011112 |
| Allomalia quadrivirgata | 00211200002002020201100000001011112 |
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| Mesocordylus bracteolatus | 11221101101002022201100000021111103 |
| Yuccaborus frontalis | 11221101101002022001100000021111103 |
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| Rhynchophorus palmarum | 11220101101002012001100000021111103 |
| Otidognathus sp | 11220101101002012001100000021111103 |
| Diocalandra frumenti | 11220101101002042201100000021111103 |
| Toxorhinus baonii | 11220101101002042201100000021111103 |
| Sitophilus oryzae | 11220101101002042201100000021111103 |
| Aphiocephalus guerini | 11221101101002022001100000021111103 |
| Ommatolampus paratasioides | 11220101101002022201100000021111103 |
| Polytus mellerborgii | 11220101101002042201100000021111103 |
| Rhodobaenus tredecimpunctatus | 11220101121002042201100000021111103 |
| Scyphophorus acupunctatus | 11220101101002022201100000021111103 |
| Strombocerinae gen. sp. | 11221101101002022201100000021111101 |
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| Grypus leechi | 11212200000002012201100000001111101 |
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| Stenopelmus rufinasus | 11211201010002012201100000001111111 |
| Tanysphyrus lemnae | 11220201000002022201100000011111102 |
| Tadius erirhinoides | 11221201000002012201100000001111102 |
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| Alaocybites sp. | 11212201000002021101100000011111102 |
| Gilbertiola sp. | 11212201002002021101100000011111102 |
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| Perieges bardus | 11112201010001011101100000011111112 |
| Antiquis opaque (French amber) | 1121120000000 2022?011000002111121 |
| Curculio pardalis | 11211200000002022201100000021111123 |
| Shigizo sp | 11211200000002022201100000021111123 |
| Carponius axillaris | 11211200000002022201100000021111123 |
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| Acentrus histrio | 11211200000002022201100000021111123 |
| Anoplus plantaris | 11211200000002022201100000021111123 |
| Cionopsis lineola | 11211200000002022201100000021111123 |

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| Camarotus sp | 11212200010001022001100002111123 |
| Odontopus calceatus | 11212200010002022201100002111123 |
| Ceratopus sp. | 11212200000002022201100002111123 |
| Cionus hortulanus | 11252200002002022201100002111123 |
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| Phyllotrox (Euclyptus) sp. | 11212200000002022201100002111123 |
| Ellescus ephippiatus | 11212200000002022201100002111123 |
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| Meriphus sp | 11212200000002022201100002111123 |
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| Isochnus rufipes | 11221200001002022201100002111123 |
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| Promecotarsus sp. | 11212200010002022201100002101123 |
| Terires sp. | 11212200010002022201100002111123 |
| Styphlus penicillus | 11212200010002022201100002101123 |
| Tychius picirostris | 11222200011002022201100002111123 |
| Lignyodes horridulus | 11212200000002022201100002111113 |
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| Pnigodes setosus | 11212200000002022201100002111123 |
| Hydronomus sinuatocollis | 11212200000002022201100002111123 |
| Baris torquata | 11211210000002022201100002311133 |
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| Limnobaris bicincta | 11212210000002022201100002311133 |
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| Eisonyx crassipes | 11211210000002022201100002311133 |
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| Thanius sp. | 11211210000002022201100002311133 |
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| Pelenomus roelofsi | 11222200011002022211100002111143 |
| Rhinoncus perpendicularis | 11212200010002022211100002111143 |
| Scleropterus serratus | 11221200001002022211100002311143 |
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| Amalus scortillum | 11221200001002022211100002311143 |
| Ceutorhynchus nitidulus | 11211200000002022211100002311143 |
| Cardipennis sulcithorax | 11211200000002022211100002311143 |
| Dieckmannius sexnotatus | 11211200000002022211100002311143 |
| Coeliodes rana | 11211200000002022211100002311143 |
| Mecysmoderes euglyptus | 11221200001002022211100002311143 |
| Xenysmoderodes sasajii | 11221210001002022211100002311143 |
| Augustinus comes | 11211200000002022211100002311143 |
| Auleutes epilobii | 11211200000002022211100002311143 |
| Cyphosenus citricola | 11211200000002022211100002311143 |

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| Lioxyonyx fausti | 112112000000020222111000002311143 |
| Arachnobas gazella | 112112100000020222011000002311143 |
| Campyloscelus westermanni | 112112101000020222011000002311123 |
| Metialma straminea | 112112100000020222011000002211143 |
| Cyllophorus fausciatus | 112112100000020222011000002211143 |
| Acoptus suturalis | 112122100000020222011000002211143 |
| Lobotrachelus troglodytes | 112122100000020221011000002211143 |
| Mecopus trilineatus | 112222100010020222011000002211143 |
| Telephae oculata | 112122100000020222011000002211143 |
| Balanogastris kolae | 112112100000020222011000002211143 |
| Cratosomus "punctulatus" | 112112000000020222011000002211143 |
| Trichodocerus sp. | 110301000100020222011000002211143 |
| Cylindrocopturus operculatus | 111102000000020222011000002211143 |
| Cylindrocopturus adspersus | 111102000000020222011000002211143 |
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| Catolethrus sp. | 112112100000020222011000001111143 |
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| Heptarthrum sp. | 112112000000020222011000002111143 |
| Phloeophagus minor | 112112000000020222011000002111143 |
| Cryptorhynchus lapathi | 112112000000020222011000002301143 |
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| Eurhoptus sp. | 112112000000020222011000002301143 |
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| Aedemonus erichsoni | 112112000000020222011000002301143 |
| Mechistocerus sp. | 112112000000020222011000002311143 |
| Camptorhinus sp. | 112112101000020222011000002311143 |
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| Strongylopterus ovatus | 112122100000020220011000002311143 |
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| Aegorhinus nodipennis | 112122000100020212011000002111143 |
| Diabathrarius sp. | 112122000100010220011000002311143 |
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| Listroderes costirostris | 112122000100020212011000012111143 |
| Agraphus bellicus | 112222000110011212011001012111143 |
| Lepidophorus lineaticolllis | 112122000100020212011000002111143 |
| Anypotactus jansoni | 112122000100011212011001012111143 |
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| Brachyderes lusitanicus | 112122000100011212011001012111143 |
| Trigonops platessa | 112122000100011212011001002111143 |
| Cneorrhinus geminatus | 112122000100011212011000012111143 |
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| Cyrtepistomus castanaeus | 112122000100011212011000112111143 |
| Palirhoeus eatoni | 112122000100010212011000002111143 |
| Elytrurus griseus | 112122000100011212011000112111143 |
| Episomus lentus | 112222000110011212011001012111143 |
| Eudiagogus pulcher | 112122000100011212011001012111143 |
| Colecerus (Coleocerus) marmoratus | 112122100100011212011001012110143 |
| Eucoleocerus (Eucolecerus) sp. | 112122100100011212011001012110143 |
| Eupholus bennetti | 112122000100021210011001012110143 |
| Compsus argyreus | 112122000100011212011001012110143 |

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| Hormorus undulatus | 112122000100021212011001012111143 |
| Leparocerus morio | 112122000100011212011001012111143 |
| Hypoptus macularis | 112122000100021212011000112111143 |
| Cyrtomon (Cyphus) lautus | 112122000100011212011001012111143 |
| Naupactus (Graphognathus) peregrinus | 112122000100011212011001012111143 |
| Ophryastes (Eupagoderes) argentatus | 112122000100021212011001012110143 |
| Sciopithes obscurus | 112122000100011212011001012111143 |
| Pachyrrhynchus tobafolius | 112122000100011232011000002111143 |
| Stomodes gyrosicollis | 112122000100010212011000012111143 |
| Rhinospathe albomarginata | 112122000100021212011000112110143 |
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| Mitostylus tenius | 112122000100011210011000112111143 |
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| Apleurus (Dinocleus) molitor | 112122000000020222011000002111143 |
| Stephanocleonus sp. | 112122000100021221011000112111143 |
| Rhinocyllus conicus | 112122000100021222011000102111143 |
| Bangasternus orientalis | 112122000100021222011000102111143 |
| Laemosaccus nephele | 112112000100020222011000002111143 |
| Neolaemosaccus (Saccolaemus) carinicollis | 112112000000020222011000002111143 |
| Magdallis armicollis | 112122000000020222011000002111143 |
| Liparus glabrirostris | 112122000100020212011000002111143 |
| Acicnemis sp. | 112112100000020222011000002111143 |
| Amorphocerus sp. | 112112000000020222011000002111143 |
| Rhyparonotus sp. | 112122000140020222011000002111143 |
| Cholus rana | 112112000000020222011000002311143 |
| Rhyssomatus lineaticollis | 112212000000020222011000102311143 |
| Cleogonus sp. | 112222100000020222011000002311143 |
| Conotrachelus fissunguis | 112122100000020222011000002311143 |
| Gononotus angulicollis | 112112000000020222011000002311143 |
| Guioperus trifasciatus | 112112000000020222011000002311143 |
| Heilus bioculatus | 112112000000020220011000002311143 |
| Heilipodus polygluttatus | 112112000000020220011000002311143 |
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| Sclerocardius africanus | 112112100000020222011000002311143 |
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| Neophycoroetes testaceus | 112122000000020222011000002111143 |
| Trigonocolus curvipes | 112112100000020222011000002111143 |
| Trypetes sp. | 112122000000020222011000002011143 |
| Parorobitus gibbus | 112112100000020222011000002311143 |

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| Xyleborus spathipennis | 1121010000000001010110000000111111 |
| Sphaerotrypes pila | 1121010000000001010110000000111111 |
| Alniphagus costatus | 1121010000000001010110000000111111 |
| Pityophthorus jucundus | 1121010000000001010110000000111111 |
| Hylurgops planirostris | 1121110000000101000110000000111111 |
| Tesserocerus inermis | 1125010000300101010110000000111101 |
| Scolytus multistriatus | 1021010000000101000110000000111101 |
| Platypus parallelus | 1125010000300001000100000000111111 |
| Ficicis despectus | 1121110000000101000100000000111111 |
| Dendroctonus micans | 1125110000210101010110000000111101 |
| Diapus aculeatus | 1125010000300001010100000000111111 |
| Cylindrobrotus pectinatus (Lebanese amber) | 0125010000200001000111000000111101 |
| Microborus inertus (Burmese amber) | 0125010000200001000110000000111101 |
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| indet 3 nemonychid (Yixian 2010159) | 000320?0000??2000?0??000000010100 |
| indet 2 nemonychid (Yixian 2005111) | 000320?0000??2000?0??000000010100 |
| Microprobelus liuae (Yixian 2005106) | 000320?0000??2000?0??000000010100 |
| Microprobelus liuae (Yixian 2007102) | 000310?0000??2000?0??000000010100 |
| Chinocimberis augustipecteris (Yixian 2007104) | 000320?0000??2000?0??000000010100 |
| Chinocimberis augustipecteris (Yixian 2005127) | 000320?0000??2000?0??000000010100 |
| Chinocimberis magnoculi (Yixian 2010155) | 000320?0000??2000?0??000000010100 |
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| Renicimberis latipecteris (Yixian 2005123) | 000320?0000??2000?0??000000010100 |
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| A. brachyorhinos (Yixian 2005119) | 000410?0000??2012?0??000000011101 |
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| A. macilentus (Yixian 2007103) | 000410?0000??2012?0??000000011101 |
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| A. relicinus (Yixian 2010152) | 000410?0000??2012?0??000000110101 |
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| A. relicinus (Yixian 2005117) | 000410?0000??2012?0??000000110101 |
| A. relicinus (Yixian 2005122) | 000410?0000??2012?0??000000111101 |
| A. relicinus (Yixian 2010160) | 000410?0000??2012?0??000000111101 |
| A. macilentus (Yixian 2010156) | 000410?0000??2012?0??000000111101 |
| Archaeorrhynchus acutirostris | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus latitarsus | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus paradoxopus | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus kryzhanovskyi | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus nikolaevi | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus carpenteri | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchus sukatshevai | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchoides crowsoni | 000310?0000??2000?0?0000000001000 |
| Archaeorrhynchoides arnoldii | 000310?0000??2000?0?0000000001000 |
| Kararhynchus occiduus | 000310?0000??2000?0?0000000001000 |
| Eobelus longipes | 000310?0000??2000?0?0000000001000 |
| Eobelus sp. | 000310?0000??2000?0?0000000001000 |
| Belonotaris karatavicus | 000310?0000??2000?0?0000000001000 |
| Probelus tibialis | 000310?0000??2000?0?0000000001000 |
| Probelus cockerelli | 000310?0000??2000?0?0000000001000 |
| Probelus scudderi | 000310?0000??2000?0?0000000001000 |

| | |
|---|---|
| Probelus longitarsus | 000310?0000??2000?0?0000000001000 |
| Probelus curvispinus | 000310?0000??2000?0?0000000001000 |
| Probelus handlirschi | 000310?0000??2000?0?0000000001000 |
| Probelopsis acutiapex | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus wanatavieus | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus gratshevi | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus zherichini | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus medvedevi | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus rasnitsyni | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus rohdendorfi | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus wickhami | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus korotyaevi | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus heeri | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus martynovi | 000310?0000??2000?0?0000000001000 |
| Arnoldibelus karatavicus | 000310?0000??2000?0?0000000001000 |
| Nanophydes ovatus | 000310?0000??20?0?0?0000000001000 |
| Ampliceps dentitibia | 000410?0000??20?0?0?0000000001000 |
| Ampliceps furcitibia | 000410?0000??20?0?0?0000000001000 |
| Oxycorynoides progressivus | 000410?0000??20?0?0?0000000001000 |
| Karataucarodes zimmermanni | 000410?0000??20?0?0?0000000001000 |
| Scelocamptus dubius | 000410?0000??20?0?0?0000000001000 |
| Scelocamptus curvipes | 000410?0000??20?0?0?0000000001000 |
| Oxycorynoides rohdendorfi | 000310?0000??20?0?0?0000000001000 |
| Oxycorynoides brevipes | 000310?0000??20?0?0?0000000001000 |
| Oxycorynoides zherichini | 000310?0000??20?0?0?0000000001000 |
| Oxycorynoides similis | 000310?0000??20?0?0?0000000001000 |
| Belonartis lineatipunctatus | 000310?0000??20?0?0?0000000001000 |
| Oxycorynoides mongolicus | 000310?0000??20?0?0?0000000001000 |
| Oxycorynoides gurvanensis | 000310?0000??20?0?0?0000000001000 |
| Eccoptarthroides longirostris | 000310?0000??2000?0?0000000001000 |
| Eccoptarthroides ponomarenkoi | 000310?0000??2000?0?0000000001000 |
| Eccoptarthroides martynovi | 000310?0000??2000?0?0000000001000 |
| Eccoptarthroides nikitskyi | 000310?0000??2000?0?0000000001000 |
| Pseudobrenthorrhinus magnus | 000310?0000??2000?0?0000000001000 |
| Pseudobrenthorrhinus crassicornis | 000310?0000??2000?0?0000000001000 |
| Brenthorrhinus mirabilis | 100320?0000??2000?0?0000000001000 |
| Gobibrenthorrhinus gigas | 000310?0000??2000?0?0000000001000 |
| Brenthorrhinus brevirostris | 000310?0000??2000?0?0000000001000 |
| Brenthorrhinoides mandibulatus | 000310?0000??2000?0?0000000001000 |
| Scelocamptus tenuirostris | 000310?0000??2000?0?0000000001000 |
| Brenthorrhinoides robustus | 000310?0000??2000?0?0000000001000 |
| Brenthorrhinoides pubescens | 000310?0000??2000?0?0000000001000 |
| Mongolbrenthorrhinus arnoldii | 000410?0000??2000?0?0000000010100 |
| Mongolbrenthorrhinus pusillus | 000410?0000??2000?0?0000000010100 |
| Mongolbrenthorrhinus flavus | 000410?0000??2000?0?0000000010100 |
| Testudobrenthorrhinus baissiensis | 000410?0000??2012?0?0000000011100 |
| Testudobrenthorrhinus taetricus | 000410?0000??2012?0?0000000011100 |
| Buryatnemonyx niger | 000410?0000??2012?0?0000000011100 |
| Buryatnemonyx tener | 000410?0000??2012?0?0000000011100 |
| Buryatnemonyx gratshevi | 000410?0000??2012?0?0000000011100 |
| Oxycorynoides ponomarenkoi | 000410?0000??2012?0?0000000011100 |
| Procurculio fortipes | 000420?0000??2000?0?0000000010100 |
| Procurculio pallens | 000420?0000??2000?0?0000000010100 |
| Megabrenthorrhinus grandis | 000410?0000??2000?0?0000000010100 |
| Megabrenthorrhinus longicornis | 000410?0000??2000?0?0000000010100 |
| Eccoptarthrus crassipes | 000410?0000??2000?0?0000000010100 |
| Eccoptothorax latipennis | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus pallidirostris | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus ovatus | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus arnoldii | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus elongatus | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus rotundicollis | 000410?0000??2000?0?0000000010100 |

| | |
|---|---|
| Distenorrhinus angulatus | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus major | 000410?0000??2000?0?0000000010100 |
| Distenorrhinus antennatus | 000420?0000??2000?0?0000000010100 |
| Paroxycorynoides elegans | 000410?0000??2000?0?0000000010100 |
| Selengarhynchoides sharyngolensis | 000410?0000??2000?0?0000000011100 |
| Selengarhynchus ovalis | 000410?0000??2000?0?0000000011100 |
| Pseudonemonyx stupendus | 000420?0000??2000?0?0000000010100 |
| Cretonemonyx minimus | 000420?0000??2000?0?0000000010100 |
| Cretonemonyx longirostris | 000420?0000??2000?0?0000000010100 |
| Cretonemonyx profligatus | 000420?0000??2000?0?0000000010100 |
| Megametrioxenoides longus | 000410?0000??2000?0?0000000011100 |
| Megametrioxenoides proelomus | 000410?0000??2000?0?0000000011100 |
| Cretoxenoides erdeniensis | 000410?0000??2000?0?0000000011100 |
| Chinocimberis dispersus | 000420?0000??2000?0?0000000010100 |
| Baissimberis prodigiosus | 000420?0000??2000?0?0000000010100 |
| Mongolocar orcinus (nemonychid) | 010410?0000??2012?01?000000111101 |
| Karacar contractus (nemonychid) | 010410?0000??2012?01?000000111101 |
| Baissabrenthorrhinus mirabilis | 010410?0000??2012?01?000000111101 |
| Ulyaniana nobilis | 0004200000?1200??000000000010101 |
| Ulyaniana excellens | 0004200000?1200??000000000010101 |
| Ulyanisca dentipes | 0004200000?1200??000000000010101 |
| Slonik sibiricus | 0004200000?1200??0???0???011?10? |
| Hyperites nadezhkini | 000?200010?12?0???????????11?10? |

TABLE 2. Characters 33 - 65

| | |
|---|---|
| | 33   38   43   48   53   58   63 |
| | \|    \|    \|    \|    \|    \|    \| |
| Cucujus clavipes | 000000000001201230000102432000011 |
| Orsodacne atra childreni (Orsodacnidae) | 000000000000201130000100430000011 |
| Fidia viticida (Chrysomelidae) | 000000000001201030000100430000011 |
| Cimberis sp. | 000000000000001130500100430000001 |
| Nannomacer germaini | 000000000000001130500100430000011 |
| Mecomacer scambus | 000300000000001130500101432000001 |
| Rhynchitomacerinus kuscheli | 000300000000001130500101432000001 |
| Nemonyx lepturoides | 000000000000000020000100430001002 |
| Doydirhynchus austriacus | 000000001000001030500101430000002 |
| Lecontellus byturoides | 000000001000001030500110432000001 |
| Arra similis (Spanish amber) | 0003000000000?0??3?0?0102430000011 |
| indet 5 anthribid (Yixian 2005126) | 00?3?00000?1?0????2?0102??10?00?? |
| Trigonorhinus sp. | 000010000001001020600102201001011 |
| Anthribus nebulosus | 000010000000000020600102201001000 |
| Epicerastes sp. | 000000000000000020600102111002000 |
| Apolecta samarana | 000000000000000020600102111002000 |
| Gynandrocerus sp. | 000010000000000020600102321001000 |
| Phaenithon semigriseum | 000010000001001020600102221002000 |
| Basitropis sp. | 000010000000000020600102321001000 |
| Strabus bimaculatus | 000000000000000020600102111002000 |
| Corrhecerus sp | 000010000000000020600102311001000 |
| Straboscopus tessellatus | 000000000000000020600102221002000 |
| Euparius marmoreus | 000010000001001020600102211001011 |
| Discotenes nigrotuberculata | 000000000001001020600102101002011 |
| Ischnocerus infuscatus | 000000000000000020601102111002000 |
| Dendropemon sp. | 000000000000000021600102211001000 |
| Eucorynus crassicornis | 000000000000000021600102211001000 |
| Gymnognathus sp. | 000000000000000020600102121002011 |
| Dinema filicornis | 000010000000000020600102301002001 |
| Neseonos brunneus | 000010000000000020600102302002001 |
| Mauia subnotata | 000010000000000021600102201001000 |
| Illis anna | 000000000000000021600102201001000 |
| Mecocerus sp. | 000000100000000021600102121002000 |
| Acanthothorax basalis | 000000100000000021600102121002000 |

| | |
|---|---|
| Phloeophilus sulcifrons | 00000010000000000216001021210020000 |
| Mycetis marginicollis | 00000010000000000216001021110020000 |
| Ormiscus sp. | 00001000000000000206001022110020011 |
| Ozotomerus bipunctatus | 00001000000000000206011022010010000 |
| Piesocorynus sellatus | 00000000000100002060010231100100 0 |
| Brachycorynus distentus | 00000000000000000206001022110020000 |
| Goniocloeus sp. | 00030000000100002060010210100200 0 |
| Platyrhinus resinosus | 00000010000000000216001022210020000 |
| Phoenicobiella chamaeropis | 00030000000000010206001021110020000 |
| Toxonotus fascicularis | 00001000002000002160010220100100 0 |
| Phloeobius pallipes | 00001000000000000216001022010010000 |
| Platystomos wallacei | 00001000000000000216001022010010000 |
| Ptychoderes sp. | 00000000000000000206001022010020000 |
| Phloeotragus polyopras | 00000000000000000216001021110020000 |
| Cerambyrhynchus schoenherri | 00000000000000000216001022010020000 |
| Rhinotropis superciliaris | 00000010000000000216001022110020000 |
| Sintor quadrilineatus | 00030000000000000216001022110020000 |
| Allandrus bifasciatus | 00000000000000000216001022010020000 |
| Stenocerus sp. | 00030000000000000216001022110020000 |
| Plintheria plintheroides | 00000000000000000216001022110020000 |
| Trigonorhinus sticticus | 00000000000000000216001022010010000 |
| Tropideres fasciatus | 00030010000000000216001021110020000 |
| Acorynus pallipes | 00000010000000000216001021110020000 |
| Cedus guttatus | 00000010000000000216001022110020000 |
| Xenocerus ancyra | 00001000000000000216001023110020000 |
| Xylinada rugicollis | 00001000000000010206001023020020001 |
| Stiboderes westermanni | 00001000000000000226001023110020000 |
| Exechesops bakeri | 00001000000000000216001020010020000 |
| Holostilpna sp. | 00001010000000000216001020010010000 |
| Choragus sayi | 00010000000000000216001012010010000 |
| Euxenus jordani | 00010000000000000216001022010010000 |
| Araecerus levipennis | 00001010000000000216001022010010000 |
| Acaromimus americanus | 00000000100000000216001022010010000 |
| Misthosima sp. | 00000000100000000216001022010010000 |
| Cisanthribus sp. | 00000000100000000216001023010010000 |
| Notioxenus ater | 00000000100000000216001020110020000 |
| Urodon rufipes | 00001000000000000216001010010010000 |
| Rhinotia sp. | 00030000000100103001011043100000 1 |
| Belus semipunctatus | 10000100000100103001010043100000 1 |
| Homalocerus lyciformis | 10000000000100103000011043000000 1 |
| Pachyura australis | 00000000000100103001011043100000 1 |
| Dicordylus marmoratus | 00000000000100103000010043000000 1 |
| Daohugou belid sp. | 0?00000000?1?0????00010043000000?1 |
| Montsecbelus solutus | ???0000000?1?0??????0100??10?00?? |
| Car sp. | 20000000000100110000010043000000 1 |
| Car condensatus | 20000001000100110000010043000000 1 |
| Caenominurus topali | 20100100000100110000010043000000 1 |
| Albicar contriti (Spanish amber) | 1?0001000001?0????0?010043000000?1 |
| Chilecar pilgerodendri | 20100100000100110000010043000000 1 |
| Carodes revelatus | 20100000000100110000010043100000 1 |
| Baissorhynchus tarsalis | 0001000000?1?0????0?01004300?00?? |
| Paleocar princeps | 0000000000?1?0??0?0?0101??00?00?? |
| Baissacar passarius | 0000000000?1?0??0?0?01014300?00?? |
| Cretonanophyes longirostris | 0001000000 1?0????0?01004300?00?? |
| Cretonanophyes punctatus | 0001000000 1?0??????????43??????? |
| C. punctatus (Yixian 2007105 1/2) | 00?3?00000?1?0????0?0101??20?00?? |
| C. punctatus (Yixian 2006103) | 00?3?00000?1?0????0?0100??00?00?? |
| C. punctatus (Yixian 2005115) | 00?3?00000?1?0????0?0100??00?00?? |
| C. punctatus (Yixian 2010158) | 00?3?00000?1?0????0?0100??00?00?? |
| C. zherikhini (Yixian 2006101) | 00?3?00000?1?0????0?0100??00?00?? |
| C. zherikhini (Yixian 2005113) | 00?3?00000?1?0????0?0100??00?00?? |
| C. zherikhini (Yixian 2005114) | 00?3?00000?1?0????0?0100??00?00?? |

| | |
|---|---|
| C. zherikhini (Yixian 2005109) | 00?3?00000?1?0????0?0100??00?00?? |
| C. zherikhini (Yixian 2005112) | 00?3?00000?1?0????0?0100??00?00?? |
| C. zherikhini (Yixian 2005103) | 0001?00000?1?0??0?0?0100??00?00?? |
| Cretonanophyes asiaticus (sp1) | 00010000001?0????0?01004300?00?? |
| Cretonanophyes neocomicus (sp2) | 00010000001?0????0?01004300?00?? |
| Jarzembowskia edmundi | 0?00000?00?1?0????0?01?0??00?00?? |
| Baissacarodes sibiricus | 0001000000?1?0????0?01004300?00?? |
| Emanrhynchus lebedevi | 0001000000?1?0????0?0100??00?00?? |
| Gobicar ponomarenkoi | 0003000000?1?0????0?01014310?00?? |
| Gobicar ulugeiensis | 0003000000?1?0????0?01014310?00?? |
| Mesophyletis calhouni | ??000000001?0????0?01004300?00?? |
| Hispanocar kseniae | ???0000000?1?0????0?0100??00?00?? |
| Martinsnetoa dubia | ???0000000?1?0??????0100??10?00?? |
| Cretocar luzzii | ???0010000?1?0????0?01004300?0000 |
| Montsecanomalus zherikhini | ???0000000?1?0????0?0100??00?0000 |
| Zigras cornus | 1?0001000001?0???00?01004300?0000 |
| Zigras nudicornus | 1?0001000001?0???00?01004300?0000 |
| Scabridus implexus | 1?0000000001?0???00?01004300?0000 |
| Scabridus zigrasi | 1?0000000001?0???00?01004300?0000 |
| Anchineus dolichobothris | ???001000001?0????0?01004300?00?? |
| Caridae 1 | ??00000?00?1?0????0?0100??00?00?? |
| Caridae 2 | ??00000000?1?0????0?0100??00?00?? |
| Caridae 3 | 1?00000000?1?0????0?0100??00?00?? |
| Preclarusbelus vanini | ???0010000?1?0????0?0100??10?00?? |
| Arariperhinus monnei | ???0000000?1?0??????0100??00?00?? |
| Gratshevbelus erici | ???0010000?1?0????0?0100??00?00?? |
| Proterhinus sp. | 000000001001001011100100432000011 |
| Rhopalotria bicolor | 000000000001001001000101432000001 |
| Parallocorynus bicolor | 000000000001001001000101432000001 |
| Baltocar succinicus | ??10000000?100????0?01104300?00?? |
| Haplorhynchites aeneus | 001300000001001100010110430000001 |
| Involvulus hirtus | 001300000001001100010110430000001 |
| Merhynchites bicolor | 001300000001011100000100430000001 |
| Eugnamptus punctatus | 001300003001011100000100430000001 |
| Auletobius cassandrae | 001000000001011100010100430000001 |
| Minurus testaceus | 001000000001011100010100430000001 |
| Pseudauletes sp. | 001000000001011100010100430000001 |
| Byctiscus populi | 001000000001011100010100432000011 |
| Listrobytiscus corvinus coeruleipennis | 001000000001011100010100430000011 |
| Deporaus glastinus | 001000000001011100010100430000001 |
| Pterocolus ovatus | 000000000001001100000102431000011 |
| Homeolabus analis | 001000000001011100000100431000011 |
| Attelabus nigripes | 001000000001011100000100431000011 |
| Omolabus conicollis | 001000000001011100010100430000000 |
| Euscelus dentipes | 001000000002011100000100431000000 |
| Henicolabus octospilotus | 001000000002011100000000431000010 |
| Lamprolabus sandacanus | 001000000001011100010100430000000 |
| Euops quadrifasciculatus | 001000003002011100000100431100010 |
| Pilolabus viridans | 001000000002011100010110432100001 |
| Apoderus sp. | 001000000000011120010110431110001 |
| Parapoderus flavoebenus | 001000000000011120010110431110001 |
| Clitostylus badeni | 001000000000011120010110431110001 |
| Holapoderus hystrix | 001000000000011120010110431110000 |
| Paroplapoderus pardalis | 001000000000011120010110431110000 |
| Cynotrachelus roelofsi | 001000000000011120010110431110000 |
| Trachelophorus giraffa | 001000000000011120010110431110000 |
| Ithycerus novemboracensis | 000000000001001100000110430000001 |
| Brentus anchorago | 000001010000001101300110431010001 |
| Arrhenodes minutus | 000001010000001101300110432010001 |
| Henarrhenodes macgregori | 000001000000011101300100430010001 |
| Baryrrhynchus schroderi | 000001010000011101300100430010001 |
| Amorphocephala imitator | 000001010000001101300110431010001 |

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|---|---|
| Antliarhinites zamiae | 0000010100000001101200111432010001 |
| Cylas formicarius elegantulus | 0000010100010011012001104300100001 |
| Oncodemerus sennai | 0000010000000111013001104300100001 |
| Stereodermus latirostris | 0000010100000111013001104300100001 |
| Cerobates sexsulcatus | 0000010000000111013001104300100001 |
| Taphroderopsis oscillator | 0000010000000111013101104300100001 |
| Paratrachelizus uncimanus | 0000010100000111013001104310100001 |
| Miolispa robusta | 0000010000000111013001004300100001 |
| Nemocephalus guatemalensis | 0000010100000111013101104310100001 |
| Diuris shelfordi | 0000010000000111013001004310100001 |
| Ithystenus hollandiae | 0000010000000111013101104310100001 |
| Schizotrachelus bakeri | 0000010000000111013101104300100001 |
| Hormocerus scrobicollis | 0000010000000111013101104300100001 |
| Ulocerus sp. | 0000010100000011013001104310100002 |
| Aporhina sp. | 0010000000001001100310110430010001 |
| Apion longirostre | 0000010001010010012001004300000002 |
| Sayapion arizona | 0000010001010010012001004311000002 |
| Perapion punctinasum | 0000010001010010012001004300000002 |
| Phrissotrichum tubiferum | 0000010001010010012001004311000002 |
| Alocentron attenuatum | 0000010001010010012001004300000002 |
| Aspidapion radiolus | 0000010001010010012001004310000002 |
| Ceratapion basicorne | 0000010001010010012001004300000002 |
| Omphalapion hookeri | 0000010000010010012101004310000002 |
| Cybebus dimidiatus | 0000010001010010012001004310000002 |
| Exapion ulicis | 0000010000010010012101004310000002 |
| Ixapion herculanum | 0000010001010010012101004310000002 |
| Kalcapion flavofemoratum | 0000010001010010012001104300000002 |
| Melanapion minimum | 0000010001010010012101004310000002 |
| Malvapion malvae | 0000010001010010012001004300000002 |
| Rhopalapion longirostre | 0000010001010010012101004310000002 |
| Noterapion meorrhynchum | 0000010001010010012001004310000002 |
| Eutrichapion alakanum | 0000010001010010012001104300000002 |
| Capapion seniculus | 0000010001010010012101004310000002 |
| Stenopterapion tenue | 0000010001010010012001004310000002 |
| Trichapion gracilirostre | 0000010001010010012001104300000002 |
| Chrysapion auctum | 0000010001010010012001104300000002 |
| Protapion apricans | 0000010001010010012101104310000002 |
| Tanaos bicolor | 0000000101010010002001114320000001 |
| Nanophyes canadensis | 0000001101010010002001004310000002 |
| Dieckmanniellus nitidulus | 0000001101010010002001004310000002 |
| Corimalia tamarisei | 0000001101010010002001004310000002 |
| Allomalia quadrivirgata | 0000001101010010002001004310000002 |
| Bracycerus sp. | 0000000100010011012001014301000000 |
| Microcerus costalis | 0000000100010011012001004301000000 |
| Episus gibbosus | 0000000000000011003001004300000002 |
| Ocladius obliquesetosus | 0001000100111011011001004310002000 |
| Desmidophorus sp. | 0001000100110011011001004310002000 |
| Dryophthorus americanus | 0004000100110013011001004301100000 |
| Stenommatus sulcifrons | 0004002100110013011001004301100000 |
| Cryptoderma sp. | 2004002100110013111001004311100000 |
| Orthognathus subparallelus | 2004002100111013113001014321100001 |
| Mesocordylus bracteolatus | 1004002100111013113001004311100000 |
| Yuccaborus frontalis | 0004002100111013101001014321100000 |
| Rhinostomus thompsoni | 1004002100111013113001004311100000 |
| Rhynchophorus palmarum | 1004002100111013111001004311100000 |
| Otidognathus sp | 1004002100111013111001004311100000 |
| Diocalandra frumenti | 0004002100111013111001014311100000 |
| Toxorhinus baonii | 0004002100110013111001014311100000 |
| Sitophilus oryzae | 1004002100111013111001004311100000 |
| Aphiocephalus guerini | 0004002100111013111001014311100000 |
| Ommatolampus paratasioides | 0004002100111013111001004311100000 |
| Polytus mellerborgii | 0004002100111013111001004311100000 |

| | |
|---|---|
| Rhodobaenus tredecimpunctatus | 20040021001110131130010043111000 0 |
| Scyphophorus acupunctatus | 000400210011101311100100431110000 |
| Strombocerinae gen. sp. | 100100011011101311300100433110000 |
| Notaris (Erirrhinus) festuca | 000100010011001301300110431100002 |
| Grypus leechi | 000100010011001301300110431100002 |
| Lissorhoptrus simplex | 000100010011001301300100431100002 |
| Stenopelmus rufinasus | 000100010011001101300100430000000 |
| Tanysphyrus lemnae | 000100010011001101100100430000000 |
| Tadius erirhinoides | 100000010001001101100111432100200 |
| Philacta testacea | 000000000001101101100100432100000 |
| Alaocybites sp. | 100-0---200100110130010043010020 0 |
| Gilbertiola sp. | 100-0---2001001101300100430100100 |
| Schizomicrus caecus | 100-0---2001001101300101430100100 |
| Perieges bardus | 100000010011001101300100432000100 |
| Antiquis opaque (French amber) | 1000001000?1?0??0?1?0100430000000 |
| Curculio pardalis | 100000110011001301100011431100010 |
| Shigizo sp | 100000110011001301300000431100100 |
| Carponius axillaris | 100000110011101301300000431100000 |
| Timola sp | 100000110011001301300001431100000 |
| Acalyptus carpini | 100000100011001301300101430100002 |
| Amorphoidea lata | 100000100011001301300101431100000 |
| Acentrus histrio | 100000110011001301300100430100100 |
| Anoplus plantaris | 100000110011001301300000430100000 |
| Cionopsis lineola | 100000110011001301300000430100000 |
| Anthonomus fulvus | 100000100111001301300000431100000 |
| Camarotus sp | 100000110010001301100000432100000 |
| Odontopus calceatus | 100000110010001301100000432100000 |
| Ceratopus sp. | 100100110011101301300101431100000 |
| Cionus hortulanus | 100000110111001001300000431100100 |
| Stereonychus fraxini | 100000110011001001300000431100100 |
| Haplonyx scutellatus | 100000111111101001300000431100100 |
| Derelomus basalis | 100000111011001001100101431100000 |
| Phyllotrox (Euclyptus) sp. | 100000100011101001300101431100000 |
| Ellescus ephippiatus | 100000100011001001300101431100100 |
| Dorytomus mucidus | 100000110011001301300001432100000 |
| Sicoderus tinamus | 000100110011001301300000432010000 |
| Ludovix fasciatus | 000000110011001301100000432110000 |
| Rhopalomerus tenuirostris | 000000100111001301300100430100000 |
| Meriphus sp | 000000100011001301300100430100000 |
| Geochus tibialis | 000000101011001301300100431000100 |
| Gymnaetron tetrum | 000100110011001301300101431100000 |
| Myrmex chevrolati | 100000110111001301100100430010000 |
| Piazorhinus sp. | 000000100011001101100000431100000 |
| Pyropus cyaneus | 000100110011101101300002431000010 |
| Isochnus rufipes | 000100110011001001300100430100000 |
| Tachygonus centralis | 100100110001001201100000431000000 |
| Promecotarsus sp. | 000100110001001301301000430100100 |
| Terires sp. | 000400210001001301301001430100000 |
| Styphlus penicillus | 000100110001001301300100430100000 |
| Tychius picirostris | 000000110011001301300101430100000 |
| Lignyodes horridulus | 000100110001001301300111431100000 |
| Ulomascus parallelus | 000000000111001311300102432000010 |
| Bagous transversus | 000100010001001301301100430100000 |
| Pnigodes setosus | 000100010001001301301100430100000 |
| Hydronomus sinuatocollis | 000100010011001301301100430100000 |
| Baris torquata | 100100110011101401100101431100010 |
| Anthinobaris dispilota | 100100110011001401100001431100010 |
| Limnobaris bicincta | 100100110011001401100001431100010 |
| Torcus nigrinus | 100100110011001401100011431100010 |
| Nicentrus grossulus | 100100110011001401300011431100100 |
| Calandrinus grandicollis | 100100110001001401300000431100000 |
| Eisonyx crassipes | 100100110011001401100100431100110 |

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|---|---|
| Pycnobaris pruinosa | 100100110001101401100011431100010 |
| Thanius sp. | 100100110011101401100011431100110 |
| Xystus ater | 100100110011001401100000431100210 |
| Madopterus talpa | 100100110011001401100011431100000 |
| Peridinetus irroratus | 100100110021001401300011431100200 |
| Barinus bivittatus | 100100110011101401300111431100110 |
| Sibariops concurrens | 100100110001001401300011431100010 |
| Diorymeropsis xanthoxyli | 100100110001001401300001431100110 |
| Mononychus punctumalbum | 000100000101101001100011431100210 |
| Pelenomus roelofsi | 010000000101001001100010431100010 |
| Rhinoncus perpendicularis | 010000000101001001100100430100210 |
| Scleropterus serratus | 000000000101001001101000430100210 |
| Rutidosoma globulus | 010000000101001001101000430100210 |
| Homorosoma asperum | 010000000101001001100000430100210 |
| Amalus scortillum | 010000000101001001100000430100010 |
| Ceutorhynchus nitidulus | 000000000101101001100000431100110 |
| Cardipennis sulcithorax | 000000010101001001101000431100110 |
| Dieckmannius sexnotatus | 010000000101001001101000431100110 |
| Coeliodes rana | 010000000111001001101000431100210 |
| Mecysmoderes euglyptus | 010000000101001001100000431100210 |
| Xenysmoderodes sasajii | 010000000101001001101010431100210 |
| Augustinus comes | 010000000101101001100001431100210 |
| Auleutes epilobii | 010000000101001001100000431100210 |
| Cyphosenus citricola | 000000000101001001100000431000210 |
| Anthypurinus haloxylicola | 000000000101001001101000431100210 |
| Lioxyonyx fausti | 000000000101001001100000431100210 |
| Arachnobas gazella | 100100110011101401300101431100010 |
| Campyloscelus westermanni | 100000100011101401100101431100010 |
| Metialma straminea | 100200110011001401100001431000010 |
| Cyllophorus fausciatus | 100100110011101401100000431100100 |
| Acoptus suturalis | 100200110011001401100110431000100 |
| Lobotrachelus troglodytes | 100200110011001401100000431100210 |
| Mecopus trilineatus | 100200110011001401100000431000010 |
| Telephae oculata | 100200110011001401100010431100210 |
| Balanogastris kolae | 100100110011101401100011431100010 |
| Cratosomus "punctulatus" | 000100110011101301300010431100200 |
| Trichodocerus sp. | 000200110011001401101010431100210 |
| Cylindrocopturus operculatus | 100200110011001401100010431100210 |
| Cylindrocopturus adspersus | 100200110011001401300000431100210 |
| Hoplocopturus sp. | 100200110111001401300010431100210 |
| Cossonus impressifrons | 100000010021001101100101432100000 |
| Acamptus echinus | 000000010011101101301110432110100 |
| Araucarius sp. | 100100010011101101300101432110000 |
| Catolethrus sp. | 100000000011001101100101432110000 |
| Pseudopentarthrum atrolucens | 100100011011001101300101432110000 |
| Macroscytalus chisosensis | 100100011011001101300111432110000 |
| Proeces depressus | 100100011011001101100111432110000 |
| Pseudapotrepus sp. | 100400210001001401301100430100000 |
| Elassoptes marinus | 000000011001001101200100432100000 |
| Heptarthrum sp. | 000100011011101101100101432110000 |
| Phloeophagus minor | 000100011011001101300100432110000 |
| Cryptorhynchus lapathi | 001100010011001301100111431100210 |
| Coelosternus sp. | 001100010121100301101011431100210 |
| Eurhoptus sp. | 000000011111101301101110431100210 |
| Gerstaeckeria lecontei | 000100010121001301101100430100210 |
| Aedemonus erichsoni | 101100010121001301301100430100210 |
| Mechistocerus sp. | 101100010121001301100111431100210 |
| Camptorhinus sp. | 100100210011001301301110430100210 |
| Cophes obtenus | 001100010011001301101101430100210 |
| Psepholax humilis | 001100010011001301301100431100110 |
| Strongylopterus ovatus | 001100010011001401100111431100200 |
| Torneuma subpanum | 001000011101001101300100430100210 |

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|---|---|
| Bronchus (Hipporhinus) bohemani | 000100010001001401301110432110000 |
| Amycterus elongata | 000000011001001401300100432110000 |
| Aegorhinus nodipennis | 000100000001001401301100432010000 |
| Diabathrarius sp. | 001100010111101401301100432110000 |
| Gonipterus gibberus | 000100000011001401300101430110000 |
| Emphyastes fucicola | 000100010001101301301100432110000 |
| Listroderes costirostris | 001100010111001401301111430100000 |
| Agraphus bellicus | 000000001011001301300100430100000 |
| Lepidophorus lineaticolllis | 000100010011001301300100430000000 |
| Anypotactus jansoni | 001000000111001401310100430110000 |
| Strophosoma melanogrammus | 001000001101001401300100430100000 |
| Brachyderes lusitanicus | 000000000001001401300100430110000 |
| Trigonops platessa | 000000000001001401300101430110000 |
| Cneorrhinus geminatus | 000000000101001401300100430110000 |
| Cratopus viridisparsus | 001300000111001401300101430110000 |
| Cyrtepistomus castanaeus | 001000100111001101300100430110000 |
| Palirhoeus eatoni | 000000000001001401300100430110000 |
| Elytrurus griseus | 001000010111001401300101430000000 |
| Episomus lentus | 000000001001001401300100430110000 |
| Eudiagogus pulcher | 001000000121001401301101430110000 |
| Colecerus (Coleocerus) marmoratus | 001000000111001301301101430000000 |
| Eucoleocerus (Eucolecerus) sp. | 001100010111001301301101430000000 |
| Eupholus bennetti | 000000000101001301300111430100000 |
| Compsus argyreus | 011000000111001001300100430110000 |
| Lachnopus floridanus | 011000000101001001300100430110000 |
| Hormorus undulatus | 000000000011001001300100430110000 |
| Leparocerus morio | 001000001121001001300100430000000 |
| Hypoptus macularis | 000100010021001301301100430110000 |
| Cyrtomon (Cyphus) lautus | 000000001001001001300100430110000 |
| Naupactus (Graphognathus) peregrinus | 000000001001001001300100430110000 |
| Ophryastes (Eupagoderes) argentatus | 000100010101001001301100430110000 |
| Sciopithes obscurus | 001000001111001301300100430110000 |
| Pachyrrhynchus tobafolius | 000000010001001001300100430110000 |
| Stomodes gyrosicollis | 000000001101001301300100430110000 |
| Rhinospathe albomarginata | 000000000011001001300100430110000 |
| Liophloeus nubilis | 001000010111001001300100430110000 |
| Premnotrypes vorax | 001100010111001001301101430110000 |
| Prypnus scutellaris | 000100001111001001300100430110000 |
| Rhyncogonus gracilis | 000000000111001001300100430110000 |
| Mitostylus tenius | 001000010111001301300100430110000 |
| Sitona californicus | 001300000101001301300100430110000 |
| Pachnaeus litus | 001000000111001301300100430110000 |
| Tanyrhynchus sp. | 001000010111001301301100430110000 |
| Trachyphloeus aristatus | 000000010111001301300100430110000 |
| Rhigopsis effracta | 001100010101001001301100430110000 |
| Dasydema hirtella | 001100010111001001301100430110000 |
| Hypera punctata | 001100010111001001301100431000000 |
| Coniatus tamaricis | 000000000001001001300110432000000 |
| Tylopterus pallidus | 000100110001001001300110431000000 |
| Cepurellus cervinus | 001100110101001001300101431000000 |
| Lixus concavus | 101100010111101401300001431100000 |
| Larinus carlinae | 101100010111101401300001431100000 |
| Apleurus (Dinocleus) molitor | 101100010111101401300001431100000 |
| Stephanocleonus sp. | 101100010111101401301001431100000 |
| Rhinocyllus conicus | 101100010111101401300001431100000 |
| Bangasternus orientalis | 101100010111101301301000431100100 |
| Laemosaccus nephele | 000100010011101401301010432100000 |
| Neolaemosaccus (Saccolaemus) carinicollis | 000100010011101401300010432100000 |
| Magdallis armicollis | 000100010011101401300010432100000 |
| Liparus glabrirostris | 001100010111101401300110431100000 |
| Acicnemis sp. | 000100010011001401301000431100000 |
| Amorphocerus sp. | 100100000011101101300101431100000 |

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|---|---|
| Rhyparonotus sp. | 0001000111010011013011004301000000 |
| Cholus rana | 0010000100111013013000014311000000 |
| Rhyssomatus lineaticollis | 0001000100111014013010114311001111 |
| Cleogonus sp. | 1014002101110013013000014311001000 |
| Conotrachelus fissunguis | 1001000101111014011010014311001000 |
| Gononotus angulicollis | 0010000011210013013001014301000000 |
| Guioperus trifasciatus | 0001000100110013011001104311002100 |
| Heilus bioculatus | 0011000100111013013010004311000000 |
| Heilipodus polygluttatus | 1011000100111013013000004311000000 |
| Hylobius pales | 0011000100111013013010104311000000 |
| Ithyporus stolidus | 1011000100111013013011004301001000 |
| Sclerocardius africanus | 1011000101111013013011114321002000 |
| Lepyrus palustris | 0010000101111013013001114311000000 |
| Lymantes sandersoni | 1001010110010013011001004301000000 |
| Alcidodes dentipes | 0001000100111011013010004311000000 |
| Nettarhinus bilobus | 0001000101011013013011104321001000 |
| Petalochilus gemellus | 0011000101111013013000124321000000 |
| Phrynixus sp. | 0001000011010014013001004301000000 |
| Pissodes strobi | 0011000101110011013001114311000000 |
| Sternechus paludatus | 0011000101111014013000014311000000 |
| Neophycoroetes testaceus | 0000000110010014013001014301000000 |
| Trigonocolus curvipes | 0013000001111011013000114311000000 |
| Trypetes sp. | 0011000001111013013000014321000000 |
| Parorobitus gibbus | 1001000101110014011000004311002000 |
| Scolytogenes expers | 0101100100102004014001024310000000 |
| Scolytoplatypus tycon | 0104000100002004014001020330000000 |
| Xyleborus spathipennis | 0104100100002004014001014310000000 |
| Sphaerotrypes pila | 0104100100102004014001020310020000 |
| Alniphagus costatus | 0104100100102004014001014310000000 |
| Pityophthorus jucundus | 0104100100102004014001022310000000 |
| Hylurgops planirostris | 0004000100100013014001114310000000 |
| Tesserocerus inermis | 0104000100102013013101014330000000 |
| Scolytus multistriatus | 0104100101002013016001022310000000 |
| Platypus parallelus | 0100000000102014012101014330000000 |
| Ficicis despectus | 0104100100102013014001114310000000 |
| Dendroctonus micans | 0104000100101013014001114310000000 |
| Diapus aculeatus | 0100000000102014012101004330000000 |
| Cylindrobrotus pectinatus (Lebanese amber) | 0104100100102004012001010330000000 |
| Microborus inertus (Burmese amber) | 0104100100102004012001024330000000 |
| indet 4 nemonychid (Yixian 2007104 1/2) | 00?3?00000?1?0??3?0?0101??20000?? |
| indet 3 nemonychid (Yixian 2010159) | 00?0?00000?1?0??3?0?0101??20000?? |
| indet 2 nemonychid (Yixian 2005111) | 00?0?00000?1?0??3?0?0101??20000?? |
| Microprobelus liuae (Yixian 2005106) | 00?0?00000?1?0??3?0?0101??20000?? |
| Microprobelus liuae (Yixian 2007102) | 00?0?00000?1?0??3?0?0101??20000?? |
| Chinocimberis augustipecteris (Yixian 2007104) | 00?0?00000?1?0??3?0?0101??20000?? |
| Chinocimberis augustipecteris (Yixian 2005127) | 00?3?00000?1?0??3?0?0101??00000?? |
| Chinocimberis magnoculi (Yixian 2010155) | 00?0?00000?1?0??3?0?0101??00000?? |
| Chinocimberis magnoculi (Yixian 2005107) | 00?3?00000?1?0??3?0?0101??20000?? |
| Chinocimberis augustipecteris (Yixian 2005102) | 00?3?00000?1?0??3?0?0101??20000?? |
| Renicimberis latipecteris (Yixian 2005123) | 00?3?00000?1?0??3?0?0101??00000?? |
| Renicimberis latipecteris (Yixian 2010153) | 00?3?00000?1?0??3?0?0101??20000?? |
| Renicimberis latipecteris (Yixian 2005101) | 00?3?00000?1?0??3?0?0101??20000?? |
| Renicimberis latipecteris (Yixian 2007101) | 00?0?00000?1?0??3?0?0101??00000?? |
| A. concavus (Yixian 2007105) | 00?3?00000?1?0????0?0100??00000?? |
| A. brachyorhinos (Yixian 2005105) | 000300000?1?0????0?010043000000?? |
| A. brachyorhinos (Yixian 2005119) | 00?3?00000?1?0????0?0100??00000?? |
| A. brachyorhinos (Yixian 2005125) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2007103) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2010151) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2010157) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2006102) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2005110 1/2) | 000300000?1?0????0?010043000000?? |

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|---|---|
| Abrocarina undet. 1 (Yixian 2010154) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2010152) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2005116 1/2) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2005118) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2005117) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2005122) | 00?3?00000?1?0????0?0101??00000?? |
| A. relicinus (Yixian 2010160) | 00?3?00000?1?0????0?0101??00000?? |
| A. macilentus (Yixian 2010156) | 00?0?00000?1?0????0?0101??00000?? |
| Archaeorrhynchus acutirostris | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus latitarsus | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus paradoxopus | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus kryzhanovskyi | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus nikolaevi | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus carpenteri | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchus sukatshevai | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchoides crowsoni | 0000?00030?0?0??3?0?0102??10000?? |
| Archaeorrhynchoides arnoldii | 0000?00030?0?0??3?0?0102??10000?? |
| Kararhynchus occiduus | 0000?00030?0?0??3?0?0102??10000?? |
| Eobelus longipes | 0000?00030?0?0??3?0?0102??10000?? |
| Eobelus sp. | 0000?00030?0?0??3?0?0102??10000?? |
| Belonotaris karatavicus | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus tibialis | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus cockerelli | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus scudderi | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus longitarsus | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus curvispinus | 0000?00030?0?0??3?0?0102??10000?? |
| Probelus handlirschi | 0000?00030?0?0??3?0?0102??10000?? |
| Probelopsis acutiapex | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus wanatavieus | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus gratshevi | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus zherichini | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus medvedevi | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus rasnitsyni | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus rohdendorfi | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus wickhami | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus korotyaevi | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus heeri | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus martynovi | 0000?00030?0?0??3?0?0102??10000?? |
| Arnoldibelus karatavicus | 0000?00030?0?0??3?0?0102??10000?? |
| Nanophydes ovatus | 0000?00030?0?0????0?0102??10000?? |
| Ampliceps dentitibia | 0000?00030?0?0????0?0102??10000?? |
| Ampliceps furcitibia | 0000?00030?0?0????0?0102??10000?? |
| Oxycorynoides progressivus | 0000?00030?0?0????0?0102??10000?? |
| Karataucarodes zimmermanni | 0000?00030?0?0????0?0102??10000?? |
| Scelocamptus dubius | 0000?00030?0?0????0?0102??10000?? |
| Scelocamptus curvipes | 0000?00030?0?0????0?0102??10000?? |
| Oxycorynoides rohdendorfi | 0000?00030?0?0????0?01?2??10000?? |
| Oxycorynoides brevipes | 0000?00030?0?0????0?01?2??10000?? |
| Oxycorynoides zherichini | 0000?00030?0?0????0?01?2??10000?? |
| Oxycorynoides similis | 0000?00030?0?0????0?01?2??10000?? |
| Belonartis lineatipunctatus | 0000?00030?0?0????0?01?2??10000?? |
| Oxycorynoides mongolicus | 0000?00030?0?0????0?01?2??10000?? |
| Oxycorynoides gurvanensis | 0000?00030?0?0????0?01?2??10000?? |
| Eccoptarthroides longirostris | 0000?00030?0?0??3?0?01?2??00000?? |
| Eccoptarthroides ponomarenkoi | 0000?00030?0?0??3?0?01?2??00000?? |
| Eccoptarthroides martynovi | 0000?00030?0?0??3?0?01?2??00000?? |
| Eccoptarthroides nikitskyi | 0000?00030?0?0??3?0?01?2??00000?? |
| Pseudobrenthorrhinus magnus | 0000?00030?0?0??3?0?01?2??00000?? |
| Pseudobrenthorrhinus crassicornis | 0000?00030?0?0??3?0?01?2??00000?? |
| Brenthorrhinus mirabilis | 0000?00030?0?0??3?0?01?2??20000?? |
| Gobibrenthorrhinus gigas | 0000?00030?0?0??3?0?01?2??00000?? |
| Brenthorrhinus brevirostris | 0000?00030?0?0??3?0?01?2??00000?? |

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|---|---|
| Brenthorrhinoides mandibulatus | 0000?00030?0?0??3?0?01?2??00000?? |
| Scelocamptus tenuirostris | 0000?00030?0?0??3?0?01?2??00000?? |
| Brenthorrhinoides robustus | 0000?00030?0?0??3?0?01?2??00000?? |
| Brenthorrhinoides pubescens | 0000?00030?0?0??3?0?01?2??00000?? |
| Mongolbrenthorrhinus arnoldii | 0000?00030?0?0??3?0?0??1??10000?? |
| Mongolbrenthorrhinus pusillus | 0000?00030?0?0??3?0?0??1??10000?? |
| Mongolbrenthorrhinus flavus | 0000?00030?0?0??3?0?0??1??10000?? |
| Testudobrenthorrhinus baissiensis | 0000?00030?0?0??0?0?0??1??10000?? |
| Testudobrenthorrhinus taetricus | 0000?00030?0?0??0?0?0??1??10000?? |
| Buryatnemonyx niger | 0000?00030?0?0??0?0?0??1??10000?? |
| Buryatnemonyx tener | 0000?00030?0?0??0?0?0??1??10000?? |
| Buryatnemonyx gratshevi | 0000?00030?0?0??0?0?0??1??10000?? |
| Oxycorynoides ponomarenkoi | 0000?00030?0?0??0?0?0??1??10000?? |
| Procurculio fortipes | 0000?00030?0?0??3?0?0??1??10000?? |
| Procurculio pallens | 0000?00030?0?0??3?0?0??1??10000?? |
| Megabrenthorrhinus grandis | 0000?00030?0?0??3?0?0??1??10000?? |
| Megabrenthorrhinus longicornis | 0000?00030?0?0??3?0?0??1??10000?? |
| Eccoptarthrus crassipes | 0000?00030?0?0??3?0?0??1??10000?? |
| Eccoptothorax latipennis | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus pallidirostris | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus ovatus | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus arnoldii | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus elongatus | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus rotundicollis | 0000?00030?0?0??3?0?0??1??10000?? |
| Distenorrhinus angulatus | 0000?00030?0?0??3?0?0??1??00000?? |
| Distenorrhinus major | 0000?00030?0?0??3?0?0??1??00000?? |
| Distenorrhinus antennatus | 0000?00030?0?0??3?0?0??1??10000?? |
| Paroxycorynoides elegans | 0000?00030?0?0??3?0?0??1??10000?? |
| Selengarhynchoides sharyngolensis | 0000?00030?0?0??3?0?0??2??10000?? |
| Selengarhynchus ovalis | 0000?00030?0?0??3?0?0??2??10000?? |
| Pseudonemonyx stupendus | 0003?00000???0??3?0?0102??10000?? |
| Cretonemonyx minimus | 0003?00000???0??3?0?0102??10000?? |
| Cretonemonyx longirostris | 0003?00000???0??3?0?0102??10000?? |
| Cretonemonyx profligatus | 0003?00000???0??3?0?0102??10000?? |
| Megametrioxenoides longus | 0000?00030?0?0??3?0?0??2??10000?? |
| Megametrioxenoides proelomus | 0000?00030?0?0??3?0?0??2??10000?? |
| Cretoxenoides erdeniensis | 0000?00030?0?0??3?0?0??2??10000?? |
| Chinocimberis dispersus | 0000?00030?0?0??3?0?0??2??00000?? |
| Baissimberis prodigiosus | 0000?00030?0?0??3?0?0??2??00000?? |
| Mongolocar orcinus (nemonychid) | 0000?00000?1?0??0?0?0101??00000?? |
| Karacar contractus (nemonychid) | 0000?00000?1?0??0?0?0101??00000?? |
| Baissabrenthorrhinus mirabilis | 0000?00000?1?0??0?0?0101??00000?? |
| Ulyaniana nobilis | 000300000???0??3?0?01012000000?? |
| Ulyaniana excellens | 000300000???0??3?0?01012000000?? |
| Ulyanisca dentipes | 000300000???0??3?0?01012000000?? |
| Slonik sibiricus | 0001000?00?1?0????0?01?11020000?? |
| Hyperites nadezhkini | 0000000?00?1?0??0?0?01?12000000?? |

TABLE 3. Characters 66 - 98

| | 66 71 76 81 86 91 96 |
|---|---|
| Cucujus clavipes | 020011110010001031110001111110100 |
| Orsodacne atra childreni (Orsodacnidae) | 010000110010000001010001111110100 |
| Fidia viticida (Chrysomelidae) | 120000110010001010411001111000000 |
| Cimberis sp. | 100010110010000000010001111110100 |
| Nannomacer germaini | 100010100010000000010001111110000 |
| Mecomacer scambus | 100000110010000000010001111110000 |
| Rhynchitomacerinus kuscheli | 100000110010000000010001111110000 |
| Nemonyx lepturoides | 000000110010001000010001110110000 |
| Doydirhynchus austriacus | 100000110010000000010001111110000 |
| Lecontellus byturoides | 100000110010001000010001110110000 |

| | |
|---|---|
| Arra similis (Spanish amber) | 02000?1??0?0?010????????????????00 |
| indet 5 anthribid (Yixian 2005126) | 100???1??0?????0?????????????????0 |
| Trigonorhinus sp. | 2100101300200010100100011011110100 |
| Anthribus nebulosus | 2102101100200010102100011011110100 |
| Epicerastes sp. | 2102101101200010100100011111110100 |
| Apolecta samarana | 2102101100200010102100011111110100 |
| Gynandrocerus sp. | 2102101100200010002100011011110000 |
| Phaenithon semigriseum | 2102101300200010300100011011110100 |
| Basitropis sp. | 2102101100200010102100011011110000 |
| Strabus bimaculatus | 2102101100200010202100011011110000 |
| Corrhecerus sp | 2102101100210010202100011011110000 |
| Straboscopus tessellatus | 2102101100210010202101011011110000 |
| Euparius marmoreus | 2102101100200010100100011011110100 |
| Discotenes nigrotuberculata | 2102101100200010100100011011110100 |
| Ischnocerus infuscatus | 2002101000200010102100011011110000 |
| Dendropemon sp. | 2102101000200010102100011011110000 |
| Eucorynus crassicornis | 2102101000200010102100011011110000 |
| Gymnognathus sp. | 2102101000100010100101011011110100 |
| Dinema filicornis | 2102101000200010102100011011110000 |
| Neseonos brunneus | 2102101000200010102100011011110000 |
| Mauia subnotata | 2102101000200010102100011011110000 |
| Illis anna | 2102101000200010102100011011110000 |
| Mecocerus sp. | 2102101100210010102101011011110000 |
| Acanthothorax basalis | 2102101100210010102101011011110000 |
| Phloeophilus sulcifrons | 2102101100210010102101011011110000 |
| Mycetis marginicollis | 2102101100210010202101011011110000 |
| Ormiscus sp. | 2102101000100010104100011011110100 |
| Ozotomerus bipunctatus | 2102101100200000000111012111110100 |
| Piesocorynus sellatus | 2102101000100010100110011011110100 |
| Brachycorynus distentus | 2102101100200010202100011011110000 |
| Goniocloeus sp. | 2102101000200010104110012011110100 |
| Platyrhinus resinosus | 2102101000200010100111012011110000 |
| Phoenicobiella chamaeropis | 2102101000200010100110012011110000 |
| Toxonotus fascicularis | 2102101100200010100110011011110000 |
| Phloeobius pallipes | 2102101000200010102111011011110000 |
| Platystomos wallacei | 2102101000200010102111011011110000 |
| Ptychoderes sp. | 2102101000200010000100012011110000 |
| Phloeotragus polyopras | 2102101000200010000110011011110000 |
| Cerambyrhynchus schoenherri | 2102101000200010000110011011110000 |
| Rhinotropis superciliaris | 2102101000200010102110011011110000 |
| Sintor quadrilineatus | 2102101000200010102110011011110000 |
| Allandrus bifasciatus | 2102101000200010100100012011110100 |
| Stenocerus sp. | 2102101000200010102110011011110000 |
| Plintheria plintheroides | 2102101100200010102110011011110000 |
| Trigonorhinus sticticus | 2102101000200010100100011011110100 |
| Tropideres fasciatus | 2102101000200010100111012011110100 |
| Acorynus pallipes | 2102101100200010202111011011110000 |
| Cedus guttatus | 2102101100200010202111011011110000 |
| Xenocerus ancyra | 2102101000200010000111011011110000 |
| Xylinada rugicollis | 2102101000100010100100011011110000 |
| Stiboderes westermanni | 2102101000200010100110011011110000 |
| Exechesops bakeri | 2102101000200010100100011011110000 |
| Holostilpna sp. | 1102101000100010100100011010000100 |
| Choragus sayi | 1102101000200010100100011011110000 |
| Euxenus jordani | 1102101000200010100100011011110000 |
| Araecerus levipennis | 1102101000100010300110011011110100 |
| Acaromimus americanus | 1102101000200010000100011011110000 |
| Misthosima sp. | 1102101000200010102100011011110000 |
| Cisanthribus sp. | 2102101000200010002100011011110000 |
| Notioxenus ater | 1102101000200010002100011010000000 |
| Urodon rufipes | 2102101300200010102110011111110000 |
| Rhinotia sp. | 1000001000100010200111011011110100 |

| | |
|---|---|
| Belus semipunctatus | 100000000010001000001101100110100 |
| Homalocerus lyciformis | 100000000011001001001010200110100 |
| Pachyura australis | 100000100010001020011101201110100 |
| Dicordylus marmoratus | 100000100010001020011001201110100 |
| Daohugou belid sp. | 1?????1??010?0?0????100120111010? |
| Montsecbelus solutus | 100???1??0????10???????????????0? |
| Car sp. | 100000110010001001411101001110100 |
| Car condensatus | 100000110010001001411101001110100 |
| Caenominurus topali | 100000010010001001411010101000100 |
| Albicar contriti (Spanish amber) | 100???1??0?0?010???????????????0? |
| Chilecar pilgerodendri | 100000010010001001411010101000100 |
| Carodes revelatus | 1000?00?00????10????????01?????0? |
| Baissorhynchus tarsalis | 100???1??0????00???????????????00 |
| Paleocar princeps | 100???1??0????10???????????????00 |
| Baissacar passarius | 100???1??0????10???????????????00 |
| Cretonanophyes longirostris | 100???1??0????00???????????????00 |
| Cretonanophyes punctatus | ????????????????????????????????0 |
| C. punctatus (Yixian 2007105 1/2) | 100???1??0?????0????????????????0 |
| C. punctatus (Yixian 2006103) | 100???1??0?????0????????????????0 |
| C. punctatus (Yixian 2005115) | 100???1??0?????0????????????????0 |
| C. punctatus (Yixian 2010158) | 100???1??0?????0????????????????0 |
| C. zherikhini (Yixian 2006101) | 100???0??0?????0????????????????0 |
| C. zherikhini (Yixian 2005113) | 100???1??0?????0????????????????0 |
| C. zherikhini (Yixian 2005114) | 100???1??0?????0????????????????0 |
| C. zherikhini (Yixian 2005109) | 100???1??0?????0????????????????0 |
| C. zherikhini (Yixian 2005112) | 100???1??0?????0????????????????0 |
| C. zherikhini (Yixian 2005103) | 100???1??0????00???????????????00 |
| Cretonanophyes asiaticus (sp1) | 100???1??0????00???????????????00 |
| Cretonanophyes neocomicus (sp2) | 100???1??0????00???????????????00 |
| Jarzembowskia edmundi | 100???1??0????00???????????????0? |
| Baissacarodes sibiricus | 100???1??0????00???????????????00 |
| Emanrhynchus lebedevi | 100???1??0????00???????????????00 |
| Gobicar ponomarenkoi | 100???1??0????10???????????????00 |
| Gobicar ulugeiensis | 100???1??0????10???????????????00 |
| Mesophyletis calhouni | 100???1??0????00???????????????0? |
| Hispanocar kseniae | 1?0???0??0????10???????????????0? |
| Martinsnetoa dubia | 1?0???1??0????10???????????????0? |
| Cretocar luzzii | 100???1??0????10???????????????0? |
| Montsecanomalus zherikhini | 1?0???0??0????10???????????????0? |
| Zigras cornus | 100???0??0????10???????????????00 |
| Zigras nudicornus | 100???0??0????10???????????????00 |
| Scabridus implexus | 100???0??0????10???????????????00 |
| Scabridus zigrasi | 100???0??0????10???????????????00 |
| Anchineus dolichobothris | 100???0??0????10???????????????0? |
| Caridae 1 | 10????1??0?????0???????????????00 |
| Caridae 2 | 10????0??0?????0???????????????00 |
| Caridae 3 | 100???1??0????10???????????????00 |
| Preclarusbelus vanini | 1?????0??0?????0???????????????0? |
| Arariperhinus monnei | 100???1??0?????0???????????????0? |
| Gratshevbelus erici | 100???1??0????10???????????????0? |
| Proterhinus sp. | 120110100010001010410001211110100 |
| Rhopalotria bicolor | 100000110010001011010001111110100 |
| Parallocorynus bicolor | 100000110010001010010001111110100 |
| Baltocar succinicus | 100???0??0????10???????????????0? |
| Haplorhynchites aeneus | 100000000010001001211001211110100 |
| Involvulus hirtus | 100000000010001001211001211110100 |
| Merhynchites bicolor | 100000010010001001211001111110100 |
| Eugnamptus punctatus | 100000000010001001211001111110000 |
| Auletobius cassandrae | 100000000010000001211001111110000 |
| Minurus testaceus | 100000010010000001210001111110100 |
| Pseudauletes sp. | 100000000010000001211001111110100 |
| Byctiscus populi | 100000010010001011212101211110100 |

| | |
|---|---|
| Listrobytiscus corvinus coeruleipennis | 100000010010001011212100211110100 |
| Deporaus glastinus | 100000000010001001211001111110100 |
| Pterocolus ovatus | 120000100010001011211000111110100 |
| Homeolabus analis | 100000010010000011212000111000101 |
| Attelabus nigripes | 100100010010001011212000111000101 |
| Omolabus conicollis | 100110000021201000012001111000101 |
| Euscelus dentipes | 100120110020001011212001011000101 |
| Henicolabus octospilotus | 100120110020001011212001011110101 |
| Lamprolabus sandacanus | 100110000021201011212001111000101 |
| Euops quadrifasciculatus | 100110110020001011212001011110100 |
| Pilolabus viridans | 100100110010001011212001011110100 |
| Apoderus sp. | 100110000010001011212001011000100 |
| Parapoderus flavoebenus | 100110000010001011212001011000100 |
| Clitostylus badeni | 100110000010001011212001011000100 |
| Holapoderus hystrix | 100100000010001011212001011000100 |
| Paroplapoderus pardalis | 100100000010001011212001111000100 |
| Cynotrachelus roelofsi | 102100000010001011212001011000100 |
| Trachelophorus giraffa | 100100000010001011212001111000100 |
| Ithycerus novemboracensis | 100300000020000001210001111000100 |
| Brentus anchorago | 220111101020001021410001111110000 |
| Arrhenodes minutus | 220111101020001021410001111110000 |
| Henarrhenodes macgregori | 220011111020201001410101111110000 |
| Baryrrhynchus schroderi | 220011111020201011410101111110000 |
| Amorphocephala imitator | 220111101020001021410001111110000 |
| Antliarhinites zamiae | 220010101020001031410101111110000 |
| Cylas formicarius elegantulus | 200101001020001031110101111110000 |
| Oncodemerus sennai | 210001101020001001210101011110000 |
| Stereodermus latirostris | 200031101020001031210101111110000 |
| Cerobates sexsulcatus | 210001101020001001210101011110000 |
| Taphroderopsis oscillator | 210001101020001001210101111110000 |
| Paratrachelizus uncimanus | 210101101020001031210101111110000 |
| Miolispa robusta | 210001101020001001210101111110000 |
| Nemocephalus guatemalensis | 210111101020001001410101111110000 |
| Diuris shelfordi | 210111101020001001410101111110000 |
| Ithystenus hollandiae | 210001101020001001210101111110000 |
| Schizotrachelus bakeri | 210001101020001001410101111110000 |
| Hormocerus scrobicollis | 210001101020001001410101111110000 |
| Ulocerus sp. | 100111101020001001210101111110000 |
| Aporhina sp. | 100101101010001001211011101110000 |
| Apion longirostre | 100000000021001001210000101000000 |
| Sayapion arizona | 100000000021001010410000101000000 |
| Perapion punctinasum | 100000000021000000410000101000000 |
| Phrissotrichum tubiferum | 100000000021001000010000101000000 |
| Alocentron attenuatum | 100000000021000000410000101000000 |
| Aspidapion radiolus | 100000000021001000410000101000000 |
| Ceratapion basicorne | 100000000021000000410000101000000 |
| Omphalapion hookeri | 100000000021001000410000101000000 |
| Cybebus dimidiatus | 100100000021001001410000101000000 |
| Exapion ulicis | 100100000021001000410000101000000 |
| Ixapion herculanum | 100100000021001000410000101000000 |
| Kalcapion flavofemoratum | 100100000021001000410000101000100 |
| Melanapion minimum | 100100000021001000410000101000000 |
| Malvapion malvae | 100000000021001000410000101000100 |
| Rhopalapion longirostre | 100000000021001000410000101000000 |
| Noterapion meorrhynchum | 100000000021001000410000101000000 |
| Eutrichapion alakanum | 100000000021001000410000101000100 |
| Capapion seniculus | 100000000021001000410000101000000 |
| Stenopterapion tenue | 100000000021001000410000101000000 |
| Trichapion gracilirostre | 100100000021001000410000101000100 |
| Chrysapion auctum | 100100000021000020410000101000100 |
| Protapion apricans | 100000000021001000410000101000100 |
| Tanaos bicolor | 100000001010000000410000111110100 |

| | |
|---|---|
| Nanophyes canadensis | 1001000000100010314100011110001OO |
| Dieckmanniellus nitidulus | 10010000001000103141000111100010O |
| Corimalia tamarisei | 1001000000100010314100011110001OO |
| Allomalia quadrivirgata | 1001000000100010314100011110001OO |
| Bracycerus sp. | 1023000000210000014000010100001OO |
| Microcerus costalis | 1023000000210010014000010100001OO |
| Episus gibbosus | 1023001000210000014000010100011OO |
| Ocladius obliquesetosus | 1213000200120012114100010100001lO |
| Desmidophorus sp. | 1213000200222012114110011010001lO |
| Dryophthorus americanus | 1201201000202010104100011101101OO |
| Stenommatus sulcifrons | 2201201000102010204100010001101OO |
| Cryptoderma sp. | 1001201000112010204100010011101OO |
| Orthognathus subparallelus | 1021201000122010004100010011101OO |
| Mesocordylus bracteolatus | 2121201100112010004100011111100OO |
| Yuccaborus frontalis | 1121201000122010104100010011100OO |
| Rhinostomus thompsoni | 2121201100112010104100011111100OO |
| Rhynchophorus palmarum | 2121001100120010204100010111100OO |
| Otidognathus sp | 2121001100120010204100010111100OO |
| Diocalandra frumenti | 1101201000122010102110011011111OO |
| Toxorhinus baonii | 1101201000122010102110010011100OO |
| Sitophilus oryzae | 2201201000222010204100010111100OO |
| Aphiocephalus guerini | 1121201010122010104100010011100OO |
| Ommatolampus paratasioides | 2121001110122010204100010111100OO |
| Polytus mellerborgii | 1201201010122010102110010011111OO |
| Rhodobaenus tredecimpunctatus | 1021201010122010104100010011100OO |
| Scyphophorus acupunctatus | 2101201110122010202110011111100OO |
| Strombocerinae gen. sp. | 1123201000122010104110010011101OO |
| Notaris (Erirrhinus) festuca | 1003001000210010212100011110001OO |
| Grypus leechi | 1021001000212010212110011010001OO |
| Lissorhoptrus simplex | 1021001000212010112110011010001OO |
| Stenopelmus rufinasus | 1023000000200010114110011010001OO |
| Tanysphyrus lemnae | 1021001000200010114110011010001OO |
| Tadius erirhinoides | 1111001100220012312110011010000lO |
| Philacta testacea | 1001001000210010114100010110000OO |
| Alaocybites sp. | 1101001000210012300100010110011OO |
| Gilbertiola sp. | 1121001000210012300100010110011OO |
| Schizomicrus caecus | 1121001000210012300100010110011OO |
| Perieges bardus | 1011001100112012114100010110001OO |
| Antiquis opaque (French amber) | 102???1??0????10?????????0?????OO |
| Curculio pardalis | 1013201100022010114100001010001OO |
| Shigizo sp | 1111201010020010214100011010001OO |
| Carponius axillaris | 2001201110020010214100111010001OO |
| Timola sp | 1001201110020010214100111010001OO |
| Acalyptus carpini | 2101201100020010114100011110001OO |
| Amorphoidea lata | 2001201100020010114100111010001OO |
| Acentrus histrio | 2011201100020010114100011010001OO |
| Anoplus plantaris | 1021201010020010114100011010001OO |
| Cionopsis lineola | 1021201010020010114100011010001OO |
| Anthonomus fulvus | 1021201010020010114100011010001OO |
| Camarotus sp | 1201201110020010214110011011101OO |
| Odontopus calceatus | 1021201000020010114110011011101OO |
| Ceratopus sp. | 1021101100020010114110011010000OO |
| Cionus hortulanus | 1011101000020010214100011010001OO |
| Stereonychus fraxini | 1011101000020010214100011010001OO |
| Haplonyx scutellatus | 1011101000020010114100011010001OO |
| Derelomus basalis | 2001101100020010114100011010000OO |
| Phyllotrox (Euclyptus) sp. | 2001101100020010114100011110000OO |
| Ellescus ephippiatus | 1011201000020010114100011010000OO |
| Dorytomus mucidus | 1001001100210010113100001010001OO |
| Sicoderus tinamus | 2021201000010010012100011010000OO |
| Ludovix fasciatus | 2021201000010010012100011010000OO |
| Rhopalomerus tenuirostris | 1001001000210010114100011110000OO |

| | |
|---|---|
| Meriphus sp | 200100100002001011410001101000000 |
| Geochus tibialis | 121100100021001031410001010110100 |
| Gymnaetron tetrum | 100100100002001011410001101000100 |
| Myrmex chevrolati | 100100100001001001410000101000000 |
| Piazorhinus sp. | 100100100002011031410001111000000 |
| Pyropus cyaneus | 222110110002011021411001101000100 |
| Isochnus rufipes | 100110100021001011410001111000100 |
| Tachygonus centralis | 100100110021001031410000111000100 |
| Promecotarsus sp. | 101100110002001011411001101000000 |
| Terires sp. | 102100110002001011411001101000000 |
| Styphlus penicillus | 201100110001001011411001101000000 |
| Tychius picirostris | 100100110001001011411001101000000 |
| Lignyodes horridulus | 100100110001001011410000101000100 |
| Ulomascus parallelus | 220120110002001031410000111000100 |
| Bagous transversus | 101100100002201011311001201000000 |
| Pnigodes setosus | 101100100002201011310001201000000 |
| Hydronomus sinuatocollis | 101100100002201011410001201000000 |
| Baris torquata | 122100110102201011412101201000101 |
| Anthinobaris dispilota | 210100110102211021412101211110101 |
| Limnobaris bicincta | 210100110101211021412101201000101 |
| Torcus nigrinus | 210100110102211011412101211000101 |
| Nicentrus grossulus | 221100110102211021412101211000101 |
| Calandrinus grandicollis | 222100110102211031411001210000100 |
| Eisonyx crassipes | 221100110102211031411001200000000 |
| Pycnobaris pruinosa | 122100110102201011412101201000101 |
| Thanius sp. | 122100110102201011412101201000101 |
| Xystus ater | 221100110102211031412101201000101 |
| Madopterus talpa | 210100110102211011412101201000101 |
| Peridinetus irroratus | 121100110102211021412101201000101 |
| Barinus bivittatus | 111100110102211021412101201000101 |
| Sibariops concurrens | 222100110102211021412101201000101 |
| Diorymeropsis xanthoxyli | 122100110102211031412101201110101 |
| Mononychus punctumalbum | 121300120112011210401000101000110 |
| Pelenomus roelofsi | 112300120112011020401001101000100 |
| Rhinoncus perpendicularis | 121300120112011030401001101000100 |
| Sclеropterus serratus | 121300120112011230001001101110110 |
| Rutidosoma globulus | 121300120112011230001001101000100 |
| Homorosoma asperum | 111300120112011030401001101000100 |
| Amalus scortillum | 112300120112011020401001101000100 |
| Ceutorhynchus nitidulus | 121300120112011030400000101000110 |
| Cardipennis sulcithorax | 111300120112011020401001101000100 |
| Dieckmannius sexnotatus | 121300120112011020401001101000100 |
| Coeliodes rana | 121300120112011230001001101000110 |
| Mecysmoderes euglyptus | 121300120102011130401000111000100 |
| Xenysmoderodes sasajii | 121300120102011130401001110000100 |
| Augustinus comes | 121300120112011231400000101000110 |
| Auleutes epilobii | 121300120112011230401001101000110 |
| Cyphosenus citricola | 121300120112011230401001101110110 |
| Anthypurinus haloxylicola | 121300120112011030401001101000100 |
| Lioxyonyx fausti | 121300120112011230401001101000110 |
| Arachnobas gazella | 221100120122201031410001111110100 |
| Campyloscelus westermanni | 122100120122201021410001101110100 |
| Metialma straminea | 100100110122011031410000201100100 |
| Cyllophorus fausciatus | 111100110102011031410000201000100 |
| Acoptus suturalis | 221100110122201031411001201000100 |
| Lobotrachelus troglodytes | 221100110122001131410001101100100 |
| Mecopus trilineatus | 120100110122001011100000201000100 |
| Telephae oculata | 111100100122011031410000201100100 |
| Balanogastris kolae | 111100100122011021410001201000100 |
| Cratosomus "punctulatus" | 121100120122201121410001201000100 |
| Trichodocerus sp. | 101100110122001130400001110100100 |
| Cylindrocopturus operculatus | 121100110122001031110001101000100 |

| | |
|---|---|
| Cylindrocopturus adspersus | 121100110122001011110001201000100 |
| Hoplocopturus sp. | 121100110102011121110001201100100 |
| Cossonus impressifrons | 120100100021001011401001201010000 |
| Acamptus echinus | 221100110022201011410001201010000 |
| Araucarius sp. | 102100110021001011311001201000000 |
| Catolethrus sp. | 220100100021201031310001211000000 |
| Pseudopentarthrum atrolucens | 220100100021201021310001201000000 |
| Macroscytalus chisosensis | 220100100021201031310001211000000 |
| Proeces depressus | 120100100021201031310001211000000 |
| Pseudapotrepus sp. | 121100120021001031410001201000000 |
| Elassoptes marinus | 210120100021201011410001111110100 |
| Heptarthrum sp. | 120100110021201011310001111101000 |
| Phloeophagus minor | 210100120021201031410001101100000 |
| Cryptorhynchus lapathi | 121000120002201211411001201000100 |
| Coelosternus sp. | 221020120002201221411001201000100 |
| Eurhoptus sp. | 121100120002201231410001111010000 |
| Gerstaeckeria lecontei | 121000120022001221410001111110000 |
| Aedemonus erichsoni | 121120100002201221311000101000110 |
| Mechistocerus sp. | 121100120002201211311001101000110 |
| Camptorhinus sp. | 221100120002201011311000101000100 |
| Cophes obtenus | 221000120002201231311001101000100 |
| Psepholax humilis | 221100120002201021411001101000100 |
| Strongylopterus ovatus | 121100110002201011311001101000100 |
| Torneuma subpanum | 121100120002201231411001101000000 |
| Bronchus (Hipporhinus) bohemani | 102100100001001011310001111110100 |
| Amycterus elongata | 102100110001001011310001101110100 |
| Aegorhinus nodipennis | 102100100021201011310001101010100 |
| Diabathrarius sp. | 101100110001201011311001101000000 |
| Gonipterus gibberus | 102100110001201011311101101000000 |
| Emphyastes fucicola | 100100110020001011410001111011100 |
| Listroderes costirostris | 101100110021001011310001101000000 |
| Agraphus bellicus | 100130110021001011410001011111100 |
| Lepidophorus lineaticolllis | 100130100021001011310001111100000 |
| Anypotactus jansoni | 100130100021001001311101101100000 |
| Strophosoma melanogrammus | 100130100021001001410101111110100 |
| Brachyderes lusitanicus | 100100100021201001411101111110100 |
| Trigonops platessa | 112100100021001031311101111111100 |
| Cneorrhinus geminatus | 100130100021001001410101111010100 |
| Cratopus viridisparsus | 100100100021201011311001111000100 |
| Cyrtepistomus castanaeus | 100100100021001001311000101000100 |
| Palirhoeus eatoni | 102130100021001011310001111010100 |
| Elytrurus griseus | 102130100021001011410101111111000 |
| Episomus lentus | 102100100021201001211101111110100 |
| Eudiagogus pulcher | 101100130021201001311001101000100 |
| Colecerus (Coleocerus) marmoratus | 101100130021201001311001101000100 |
| Eucoleocerus (Eucolecerus) sp. | 101100131021201001311001101000100 |
| Eupholus bennetti | 102100100021001001311001101010000 |
| Compsus argyreus | 100130100021001001311001101000000 |
| Lachnopus floridanus | 100130100021001001311001101000000 |
| Hormorus undulatus | 102100110021001001311001101010100 |
| Leparocerus morio | 102100100021001011411101111010100 |
| Hypoptus macularis | 101100100021201001311001101010000 |
| Cyrtomon (Cyphus) lautus | 100100100021001001311101111000000 |
| Naupactus (Graphognathus) peregrinus | 102100100021001011211101111000100 |
| Ophryastes (Eupagoderes) argentatus | 101100100021001001211101111111100 |
| Sciopithes obscurus | 102100100021001011311101111010100 |
| Pachyrrhynchus tobafolius | 102100100021001011310101111111100 |
| Stomodes gyrosicollis | 102100100021001011210101111111100 |
| Rhinospathe albomarginata | 100100100021201001311001101000000 |
| Liophloeus nubilis | 100100100021001001310001101010000 |
| Premnotrypes vorax | 101100100021201011310001111110100 |
| Prypnus scutellaris | 102100100021001001311001101000000 |

| | |
|---|---|
| Rhyncogonus gracilis | 1001001000210000014101011111110100 |
| Mitostylus tenius | 1021001000210010013111011010000000 |
| Sitona californicus | 1001001000210010014111011011110100 |
| Pachnaeus litus | 1021001000212010013111011010000100 |
| Tanyrhynchus sp. | 1021001000212010013100011110100000 |
| Trachyphloeus aristatus | 1001001000210010113101011110100100 |
| Rhigopsis effracta | 1011001000212010113101011010000100 |
| Dasydema hirtella | 1011001300212010013101011110100100 |
| Hypera punctata | 1021001300220010014121001010100000 |
| Coniatus tamaricis | 1001001300220010014121001010100000 |
| Tylopterus pallidus | 1021001300220010114121001010000100 |
| Cepurellus cervinus | 1001001300220010113121001010000100 |
| Lixus concavus | 2023001100212010114121011111000100 |
| Larinus carlinae | 2023001100212010114121011111000100 |
| Apleurus (Dinocleus) molitor | 2023001100212010114111011111000100 |
| Stephanocleonus sp. | 2023001100212010214111011110000100 |
| Rhinocyllus conicus | 2023001100212010214111011110000100 |
| Bangasternus orientalis | 2013001100212010214111011110000100 |
| Laemosaccus nephele | 2211001300022010214121011011100100 |
| Neolaemosaccus (Saccolaemus) carinicollis | 2221001300022010213121011011100100 |
| Magdallis armicollis | 2201001300022010113121001011100100 |
| Liparus glabrirostris | 1011001100022010114100011110100000 |
| Acicnemis sp. | 2121001000020010114100011010000100 |
| Amorphocerus sp. | 2101001100022010114120011010100100 |
| Rhyparonotus sp. | 2111001100022010114100011111100000 |
| Cholus rana | 2121001100022010214111011010000100 |
| Rhyssomatus lineaticollis | 2111001300022010114110011010000000 |
| Cleogonus sp. | 2011001300022111214110011010000110 |
| Conotrachelus fissunguis | 1011001000022010114110011010000100 |
| Gononotus angulicollis | 2101001100022010214100011110100000 |
| Guioperus trifasciatus | 1211001100022011114110011011000100 |
| Heilus bioculatus | 2011001100022010113110011011100100 |
| Heilipodus polygluttatus | 2011001100022010113110011011100100 |
| Hylobius pales | 2011001100022010114110011010000100 |
| Ithyporus stolidus | 1011001100022010213110011010000100 |
| Sclerocardius africanus | 1011001100022010113110001110000100 |
| Lepyrus palustris | 1021001000020010113100011110000100 |
| Lymantes sandersoni | 2121001100012010113100011111100000 |
| Alcidodes dentipes | 2111001100022010213110011011000100 |
| Nettarhinus bilobus | 2211001200022010214110011010000100 |
| Petalochilus gemellus | 2121001100022010113110001010000100 |
| Phrynixus sp. | 2023001200210010213100011010100000 |
| Pissodes strobi | 2123001200212010213110011010100000 |
| Sternechus paludatus | 1021001200022010013110011010000000 |
| Neophycoroetes testaceus | 2021001300212010214100010111100000 |
| Trigonocolus curvipes | 2001001001022110314121011011000100 |
| Trypetes sp. | 2201001100022010313110011111000000 |
| Parorobitus gibbus | 1213001301022111314111011010000100 |
| Scolytogenes expers | 1001001000122010110100010000000100 |
| Scolytoplatypus tycon | 1201001000121010300100011110000100 |
| Xyleborus spathipennis | 1001001000122010100100012010000100 |
| Sphaerotrypes pila | 1201001300121010300111012011000100 |
| Alniphagus costatus | 1201001000121010314100010011100100 |
| Pityophthorus jucundus | 1001001000120010010100010010100100 |
| Hylurgops planirostris | 1001001000121010314100011010000100 |
| Tesserocerus inermis | 1001001000012010104100000101100100 |
| Scolytus multistriatus | 1001101000001010100100000101100100 |
| Platypus parallelus | 1000001000001010100100110101100100 |
| Ficicis despectus | 1201001010211010314100011010000100 |
| Dendroctonus micans | 1101001000211010314100011111100100 |
| Diapus aculeatus | 1201001000001010100110110011100100 |
| Cylindrobrotus pectinatus (Lebanese amber) | 1001001000111010 1??10001011000100 |

| | |
|---|---|
| Microborus inertus (Burmese amber) | 1001001000111010???100???01??0?00 |
| indet 4 nemonychid (Yixian 2007104 1/2) | 100???1??0???0?0????????????????0 |
| indet 3 nemonychid (Yixian 2010159) | 100???1??0???0?0????????????????0 |
| indet 2 nemonychid (Yixian 2005111) | 100???1??0???0?0????????????????0 |
| Microprobelus liuae (Yixian 2005106) | 100???1??0???0?0????????????????0 |
| Microprobelus liuae (Yixian 2007102) | 100???1??0???0?0????????????????0 |
| Chinocimberis augustipecteris (Yixian 2007104) | 100???1??0???0?0????????????????0 |
| Chinocimberis augustipecteris (Yixian 2005127) | 100???1??0???0?0????????????????0 |
| Chinocimberis magnoculi (Yixian 2010155) | 100???1??0???0?0????????????????0 |
| Chinocimberis magnoculi (Yixian 2005107) | 100???1??0???0?0????????????????0 |
| Chinocimberis augustipecteris (Yixian 2005102) | 100???1??0???0?0????????????????0 |
| Renicimberis latipecteris (Yixian 2005123) | 100???1??0???0?0????????????????0 |
| Renicimberis latipecteris (Yixian 2010153) | 100???1??0???0?0????????????????0 |
| Renicimberis latipecteris (Yixian 2005101) | 100???1??0???0?0???????????????00 |
| Renicimberis latipecteris (Yixian 2007101) | 100???1??0???0?0????????????????0 |
| A. concavus (Yixian 2007105) | 100???1??0???0?0????????????????0 |
| A. brachyorhinos (Yixian 2005105) | 100???1??0???0?0???????????????00 |
| A. brachyorhinos (Yixian 2005119) | 100???1??0???0?0????????????????0 |
| A. brachyorhinos (Yixian 2005125) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2007103) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2010151) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2010157) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2006102) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2005110 1/2) | 100???1??0???0?0???????????????00 |
| Abrocarina undet. 1 (Yixian 2010154) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2010152) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2005116 1/2) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2005118) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2005117) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2005122) | 100???1??0???0?0????????????????0 |
| A. relicinus (Yixian 2010160) | 100???1??0???0?0????????????????0 |
| A. macilentus (Yixian 2010156) | 100???1??0???0?0????????????????0 |
| Archaeorrhynchus acutirostris | 000???1??0???010???????????????00 |
| Archaeorrhynchus latitarsus | 000???1??0???010???????????????00 |
| Archaeorrhynchus paradoxopus | 000???1??0???010???????????????00 |
| Archaeorrhynchus kryzhanovskyi | 000???1??0???010???????????????00 |
| Archaeorrhynchus nikolaevi | 000???1??0???010???????????????00 |
| Archaeorrhynchus carpenteri | 000???1??0???010???????????????00 |
| Archaeorrhynchus sukatshevai | 000???1??0???010???????????????00 |
| Archaeorrhynchoides crowsoni | 000???1??0???010???????????????00 |
| Archaeorrhynchoides arnoldii | 000???1??0???010???????????????00 |
| Kararhynchus occiduus | 000???1??0???010???????????????00 |
| Eobelus longipes | 000???1??0???010???????????????00 |
| Eobelus sp. | 000???1??0???010???????????????00 |
| Belonotaris karatavicus | 000???1??0???010???????????????00 |
| Probelus tibialis | 000???1??0???010???????????????00 |
| Probelus cockerelli | 000???1??0???010???????????????00 |
| Probelus scudderi | 000???1??0???010???????????????00 |
| Probelus longitarsus | 000???1??0???010???????????????00 |
| Probelus curvispinus | 000???1??0???010???????????????00 |
| Probelus handlirschi | 000???1??0???010???????????????00 |
| Probelopsis acutiapex | 000???1??0???010???????????????00 |
| Arnoldibelus wanatavieus | 000???1??0???010???????????????00 |
| Arnoldibelus gratshevi | 000???1??0???010???????????????00 |
| Arnoldibelus zherichini | 000???1??0???010???????????????00 |
| Arnoldibelus medvedevi | 000???0??0???010???????????????00 |
| Arnoldibelus rasnitsyni | 000???1??0???010???????????????00 |
| Arnoldibelus rohdendorfi | 000???1??0???010???????????????00 |
| Arnoldibelus wickhami | 000???1??0???010???????????????00 |
| Arnoldibelus korotyaevi | 000???1??0???010???????????????00 |
| Arnoldibelus heeri | 000???1??0???010???????????????00 |
| Arnoldibelus martynovi | 000???1??0???010???????????????00 |

| | |
|---|---|
| Arnoldibelus karatavicus | 000???1??0???010???????????????00 |
| Nanophydes ovatus | 000???1??0???010???????????????00 |
| Ampliceps dentitibia | 000???1??0???010???????????????00 |
| Ampliceps furcitibia | 000???1??0???010???????????????00 |
| Oxycorynoides progressivus | 000???1??0???010???????????????00 |
| Karataucarodes zimmermanni | 000???1??0???010???????????????00 |
| Scelocamptus dubius | 000???1??0???010???????????????00 |
| Scelocamptus curvipes | 000???1??0???010???????????????00 |
| Oxycorynoides rohdendorfi | 000???1??0???010???????????????00 |
| Oxycorynoides brevipes | 000???1??0???010???????????????00 |
| Oxycorynoides zherichini | 000???1??0???010???????????????00 |
| Oxycorynoides similis | 000???1??0???010???????????????00 |
| Belonartis lineatipunctatus | 000???1??0???010???????????????00 |
| Oxycorynoides mongolicus | 000???1??0???010???????????????00 |
| Oxycorynoides gurvanensis | 000???1??0???010???????????????00 |
| Eccoptarthroides longirostris | 000???1??0???010???????????????00 |
| Eccoptarthroides ponomarenkoi | 000???1??0???010???????????????00 |
| Eccoptarthroides martynovi | 000???1??0???010???????????????00 |
| Eccoptarthroides nikitskyi | 000???1??0???010???????????????00 |
| Pseudobrenthorrhinus magnus | 000???1??0???010???????????????00 |
| Pseudobrenthorrhinus crassicornis | 000???1??0???010???????????????00 |
| Brenthorrhinus mirabilis | 000???1??0???010???????????????00 |
| Gobibrenthorrhinus gigas | 000???1??0???010???????????????00 |
| Brenthorrhinus brevirostris | 000???1??0???010???????????????00 |
| Brenthorrhinoides mandibulatus | 000???1??0???010???????????????00 |
| Scelocamptus tenuirostris | 000???1??0???010???????????????00 |
| Brenthorrhinoides robustus | 000???1??0???010???????????????00 |
| Brenthorrhinoides pubescens | 000???1??0???010???????????????00 |
| Mongolbrenthorrhinus arnoldii | 100???1??0???010???????????????00 |
| Mongolbrenthorrhinus pusillus | 100???1??0???010???????????????00 |
| Mongolbrenthorrhinus flavus | 100???1??0???010???????????????00 |
| Testudobrenthorrhinus baissiensis | 100???1??0???010???????????????00 |
| Testudobrenthorrhinus taetricus | 100???1??0???010???????????????00 |
| Buryatnemonyx niger | 100???1??0???010???????????????00 |
| Buryatnemonyx tener | 100???1??0???010???????????????00 |
| Buryatnemonyx gratshevi | 100???1??0???010???????????????00 |
| Oxycorynoides ponomarenkoi | 100???1??0???010???????????????00 |
| Procurculio fortipes | 100???1??0???010???????????????00 |
| Procurculio pallens | 100???1??0???010???????????????00 |
| Megabrenthorrhinus grandis | 100???1??0???010???????????????00 |
| Megabrenthorrhinus longicornis | 100???1??0???010???????????????00 |
| Eccoptarthrus crassipes | 100???1??0???010???????????????00 |
| Eccoptothorax latipennis | 100???1??0???010???????????????00 |
| Distenorrhinus pallidirostris | 100???1??0???010???????????????00 |
| Distenorrhinus ovatus | 100???1??0???010???????????????00 |
| Distenorrhinus arnoldii | 100???1??0???010???????????????00 |
| Distenorrhinus elongatus | 100???1??0???010???????????????00 |
| Distenorrhinus rotundicollis | 100???1??0???010???????????????00 |
| Distenorrhinus angulatus | 100???1??0???010???????????????00 |
| Distenorrhinus major | 100???1??0???010???????????????00 |
| Distenorrhinus antennatus | 100???1??0???010???????????????00 |
| Paroxycorynoides elegans | 100???1??0???010???????????????00 |
| Selengarhynchoides sharyngolensis | 100???1??0???010???????????????00 |
| Selengarhynchus ovalis | 100???1??0???010???????????????00 |
| Pseudonemonyx stupendus | 100???1??0???010???????????????00 |
| Cretonemonyx minimus | 100???1??0???010???????????????00 |
| Cretonemonyx longirostris | 100???1??0???010???????????????00 |
| Cretonemonyx profligatus | 100???1??0???010???????????????00 |
| Megametrioxenoides longus | 100???1??0???010???????????????00 |
| Megametrioxenoides proelomus | 100???1??0???010???????????????00 |
| Cretoxenoides erdeniensis | 100???1??0???010???????????????00 |
| Chinocimberis dispersus | 100???1??0???010???????????????00 |

| | |
|---|---|
| Baissimberis prodigiosus | 100???1??0???010????????????????00 |
| Mongolocar orcinus (nemonychid) | 100???1??0?12010????????????????00 |
| Karacar contractus (nemonychid) | 100???1??0?12010????????????????00 |
| Baissabrenthorrhinus mirabilis | 100???1??0?12010????????????????00 |
| Ulyaniana nobilis | 100???1??0???010????????????????00 |
| Ulyaniana excellens | 100???1??0???010????????????????00 |
| Ulyanisca dentipes | 100???1??0???010????????????????00 |
| Slonik sibiricus | 000???1??0???010????????????????00 |
| Hyperites nadezhkini | 1?????1??0????10????????????????00 |

TABLE 4. Characters 99 - 131

| | 99   104  109  114  119  124  129 |
|---|---|
| Cucujus clavipes | 110103000000000010200010001001001 |
| Orsodacne atra childreni (Orsodacnidae) | 100103000000000010202010001000001 |
| Fidia viticida (Chrysomelidae) | 100022200020000000200000000012001 |
| Cimberis sp. | 110103000000000010200010003000000 |
| Nannomacer germaini | 100003000000000010202010001000000 |
| Mecomacer scambus | 110103000000000010200010001000000 |
| Rhynchitomacerinus kuscheli | 110103000000000010200010001000000 |
| Nemonyx lepturoides | 110103000000000110200000000000000 |
| Doydirhynchus austriacus | 110103000000000010100030003000001 |
| Lecontellus byturoides | 110103000000000010200010002000001 |
| Arra similis (Spanish amber) | ???????????????0????000?0???????? |
| indet 5 anthribid (Yixian 2005126) | 1????3???000????1?2?0?0?0???????? |
| Trigonorhinus sp. | 110203200030000010012010000001001 |
| Anthribus nebulosus | 110123200030000110000001000001001 |
| Epicerastes sp. | 110123200030000110000001000001001 |
| Apolecta samarana | 110123000030000110200001000001001 |
| Gynandrocerus sp. | 110023010000000110202001000001001 |
| Phaenithon semigriseum | 110103010030000010202001000001001 |
| Basitropis sp. | 110023000000000110202011000001001 |
| Strabus bimaculatus | 110023000010000100002011000001001 |
| Corrhecerus sp | 110122000010000000022001000001001 |
| Straboscopus tessellatus | 110123000000000010022001000001002 |
| Euparius marmoreus | 110023000010000110202001000001001 |
| Discotenes nigrotuberculata | 110023000030000110202001000001001 |
| Ischnocerus infuscatus | 110203000010000110002001000001001 |
| Dendropemon sp. | 110023200010000110002001000001001 |
| Eucorynus crassicornis | 110023200010000110002001000001001 |
| Gymnognathus sp. | 110103000000000110002001000001001 |
| Dinema filicornis | 110123000011000100000011000001002 |
| Neseonos brunneus | 110123000011000100003011000001001 |
| Mauia subnotata | 110123000011000100002001000001001 |
| Illis anna | 110123000011000100002001000001001 |
| Mecocerus sp. | 110003000000000110002001000001001 |
| Acanthothorax basalis | 110003000000000110002001000001001 |
| Phloeophilus sulcifrons | 110003100000000110002001000001001 |
| Mycetis marginicollis | 110203010000000110002001000001001 |
| Ormiscus sp. | 110103000030000110002001000001001 |
| Ozotomerus bipunctatus | 110003000030000110202001000001001 |
| Piesocorynus sellatus | 110123000010000110002000000001001 |
| Brachycorynus distentus | 110023000010000100002011000001001 |
| Goniocloeus sp. | 110123000010000110002001000001001 |
| Platyrhinus resinosus | 110023000010000100002001000001001 |
| Phoenicobiella chamaeropis | 110223000010000110202001000001001 |
| Toxonotus fascicularis | 110223200010000110202001000001001 |
| Phloeobius pallipes | 110023000010000110202001000001000 |
| Platystomos wallacei | 110023000010000110222001000001000 |
| Ptychoderes sp. | 100103210030000110202011000001001 |
| Phloeotragus polyopras | 110023200010000110202001000001001 |

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|---|---|
| Cerambyrhynchus schoenherri | 110023000010000110202001000001001 |
| Rhinotropis superciliaris | 110103000010000100002001000001001 |
| Sintor quadrilineatus | 110103000010000100202001000001001 |
| Allandrus bifasciatus | 110203200010000110002011000001001 |
| Stenocerus sp. | 110223000010000100202001000001000 |
| Plintheria plintheroides | 110223200010000100202001000001001 |
| Trigonorhinus sticticus | 110222200010000100202010000001001 |
| Tropideres fasciatus | 100103000000000110002001000001001 |
| Acorynus pallipes | 110123000010000100202001000001001 |
| Cedus guttatus | 110203000010000100202001000001001 |
| Xenocerus ancyra | 110003020000000110002011000001001 |
| Xylinada rugicollis | 110103210030000100202000000001001 |
| Stiboderes westermanni | 110023200000000110222011000001001 |
| Exechesops bakeri | 110103000010000100002001000001001 |
| Holostilpna sp. | 110103200030000100202000000001001 |
| Choragus sayi | 110103200010000100002001000001022 |
| Euxenus jordani | 110103200010000100002001000001022 |
| Araecerus levipennis | 100122000021000100202001000001021 |
| Acaromimus americanus | 110102200011000100002000000101022 |
| Misthosima sp. | 110122000011000100202001000001022 |
| Cisanthribus sp. | 110102200011000100002000000101022 |
| Notioxenus ater | 110123200010000100002011000001002 |
| Urodon rufipes | 110023000010000100202001000001001 |
| Rhinotia sp. | 110103200001000010200110001000001 |
| Belus semipunctatus | 110023210000000010201101000000001 |
| Homalocerus lyciformis | 110203200000000010200100000000001 |
| Pachyura australis | 110103000000000010200100001000001 |
| Dicordylus marmoratus | 110203000000000010200110000000001 |
| Daohugou belid sp. | ???????????????0????01??0???????? |
| Montsecbelus solutus | ????????????????????????0???????? |
| Car sp. | 110103000020000100202110000000002 |
| Car condensatus | 110103000020000100202110000000002 |
| Caenominurus topali | 110103200010000100000110000000002 |
| Albicar contriti (Spanish amber) | ???????????????1????01??0???????? |
| Chilecar pilgerodendri | 110103010010000100000110000000002 |
| Carodes revelatus | ?????????????????0???1??0????0??2 |
| Baissorhynchus tarsalis | 1????3???010????1?2?0?0?0???????? |
| Paleocar princeps | 1????????010????1?2?0?0?0???????? |
| Baissacar passarius | 1????????010????1?2?0?0?0???????? |
| Cretonanophyes longirostris | 1?0??3???010????1?2?0?0?0???????? |
| Cretonanophyes punctatus | 1????30????????????0????????????? |
| C. punctatus (Yixian 2007105 1/2) | 1????3???000????1?2?0?0?0???????? |
| C. punctatus (Yixian 2006103) | 1????3???010????1?2?0?0?0???????? |
| C. punctatus (Yixian 2005115) | 1????3???010????1?2?0?0?0???????? |
| C. punctatus (Yixian 2010158) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2006101) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2005113) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2005114) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2005109) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2005112) | 1????3???010????1?2?0?0?0???????? |
| C. zherikhini (Yixian 2005103) | 1????3???010????1?2?0?0?0???????? |
| Cretonanophyes asiaticus (sp1) | 1????3???010????1?2?0?0?0???????? |
| Cretonanophyes neocomicus (sp2) | 1????3???010????1?2?0?0?0???????? |
| Jarzembowskia edmundi | ????????????????????0?0?0???????? |
| Baissacarodes sibiricus | 1????3???010????1?2?0?0?0???????? |
| Emanrhynchus lebedevi | 1????3???010????1?2?0?0?0???????? |
| Gobicar ponomarenkoi | 1????3???010????1?2?0?0?0???????? |
| Gobicar ulugeiensis | 1????3???010????1?2?0?0?0???????? |
| Mesophyletis calhouni | ????????????????????0?0?0???????? |
| Hispanocar kseniae | ????????????????????????0???????? |
| Martinsnetoa dubia | ????????????????????????0???????? |
| Cretocar luzzii | ??????????????????????1?0???????? |

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|---|---|
| Montsecanomalus zherikhini | ????????????????????????0???????? |
| Zigras cornus | ????????????????????0???0???????? |
| Zigras nudicornus | ????????????????????0???0???????? |
| Scabridus implexus | ????????????????????0???0???????? |
| Scabridus zigrasi | ????????????????????0???0???????? |
| Anchineus dolichobothris | ????????????????????????????????? |
| Caridae 1 | ????????????????????0?0?0???????? |
| Caridae 2 | ????????????????????0?0?0???????? |
| Caridae 3 | ????????????????????0?0?0???????? |
| Preclarusbelus vanini | ????????????????????????0???????? |
| Arariperhinus monnei | ????????????????????2???0???????? |
| Gratshevbelus erici | ????????????????????????0???????? |
| Proterhinus sp. | 100103000-3-0-0110205130022112001 |
| Rhopalotria bicolor | 110103010000000110200110000000001 |
| Parallocorynus bicolor | 110103010000000110200110001000011 |
| Baltocar succinicus | ????????????????????0?0?0???????? |
| Haplorhynchites aeneus | 110123000010000110210000000000012 |
| Involvulus hirtus | 110123000030000110210000000000012 |
| Merhynchites bicolor | 110123000030000110010000000000012 |
| Eugnamptus punctatus | 110123010010000110210000000000012 |
| Auletobius cassandrae | 110123000030000110210000000000012 |
| Minurus testaceus | 110103000030000110210000000010012 |
| Pseudauletes sp. | 110103000000000110210000000000012 |
| Byctiscus populi | 110103000030000110010000000000012 |
| Listrobytiscus corvinus coeruleipennis | 110102001010000310010000000001022 |
| Deporaus glastinus | 110103000030000310210000000001012 |
| Pterocolus ovatus | 110123000030000110210000020012010 |
| Homeolabus analis | 110112000020000300210001000000022 |
| Attelabus nigripes | 110112000020000300210000000000012 |
| Omolabus conicollis | 110002000021000300010000000000012 |
| Euscelus dentipes | 000102010021000300020000000000012 |
| Henicolabus octospilotus | 000112010021000300010000000000012 |
| Lamprolabus sandacanus | 110002000021000300010000000000012 |
| Euops quadrifasciculatus | 110123000030000310210000000000012 |
| Pilolabus viridans | 100113010010000310210000001000012 |
| Apoderus sp. | 000113010021000310010000000000012 |
| Parapoderus flavoebenus | 000112010011000300010000000000012 |
| Clitostylus badeni | 000112010011000300010000000000012 |
| Holapoderus hystrix | 000112010021000300020000000000012 |
| Paroplapoderus pardalis | 000112010022000300010000000000012 |
| Cynotrachelus roelofsi | 000112010020000300010000000000012 |
| Trachelophorus giraffa | 000112010022000300010000000000012 |
| Ithycerus novemboracensis | 110103000010001110203030001001002 |
| Brentus anchorago | 100022110111100100223030000012002 |
| Arrhenodes minutus | 100212110111100100223030000012002 |
| Henarrhenodes macgregori | 100212120121100100203030000012002 |
| Baryrrhynchus schroderi | 100212120121100100203030000012002 |
| Amorphocephala imitator | 100012120111100100223030000012002 |
| Antliarhinites zamiae | 100002010011000100223030000012002 |
| Cylas formicarius elegantulus | 100212110111110100223030003012002 |
| Oncodemerus sennai | 100212110121100100203030000012011 |
| Stereodermus latirostris | 100212120111100100203030000012002 |
| Cerobates sexsulcatus | 100212210121100100203030000012002 |
| Taphroderopsis oscillator | 100212120121100100203030000012002 |
| Paratrachelizus uncimanus | 100212120011100100203030000012002 |
| Miolispa robusta | 100212120121100100203030000012002 |
| Nemocephalus guatemalensis | 100022110011100100223030000012002 |
| Diuris shelfordi | 100012120121100100203030000012002 |
| Ithystenus hollandiae | 100012120121100100203030000012002 |
| Schizotrachelus bakeri | 100212120121100100203030000012002 |
| Hormocerus scrobicollis | 100212110121100100203030000012002 |
| Ulocerus sp. | 100212110111100100203030000012002 |

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|---|---|
| Aporhina sp. | 100112110121100100220030000010012 |
| Apion longirostre | 100210220011010420020130000012012 |
| Sayapion arizona | 100224010111100400020130000012012 |
| Perapion punctinasum | 100212220011100400020130000012012 |
| Phrissotrichum tubiferum | 100212200111100400020130000012012 |
| Alocentron attenuatum | 100212020011100400020130000012012 |
| Aspidapion radiolus | 100212220111100400020130000012012 |
| Ceratapion basicorne | 100212220011100400020130000012012 |
| Omphalapion hookeri | 100212020131100420120130000012012 |
| Cybebus dimidiatus | 100212220010000400020130000012012 |
| Exapion ulicis | 100212020111100400120130000012012 |
| Ixapion herculanum | 100212020111100400120130000012012 |
| Kalcapion flavofemoratum | 100212010011100420120130000012012 |
| Melanapion minimum | 100212000111100400120130000012012 |
| Malvapion malvae | 100211010031100420120130000012012 |
| Rhopalapion longirostre | 100212000111100400020130000012012 |
| Noterapion meorrhynchum | 100212000131100400020130000012012 |
| Eutrichapion alakanum | 100211020031100420120130000012012 |
| Capapion seniculus | 100212000111100400020130000012012 |
| Stenopterapion tenue | 100212010111100400020130000012012 |
| Trichapion gracilirostre | 100211020031000420120131000012012 |
| Chrysapion auctum | 100211020031100420120131000012012 |
| Protapion apricans | 100211210031100420020131000012012 |
| Tanaos bicolor | 100212020010000400220131000012012 |
| Nanophyes canadensis | 100212200011000400203131010001012 |
| Dieckmanniellus nitidulus | 100202000011000400223131010001012 |
| Corimalia tamarisei | 100202000011000400223131010001012 |
| Allomalia quadrivirgata | 100202000010000400223131010001012 |
| Bracycerus sp. | 100102100---100400203030022112002 |
| Microcerus costalis | 100102100112100400203030022112002 |
| Episus gibbosus | 100102100112100400203030022112002 |
| Ocladius obliquesetosus | 100102100112100400203230022112002 |
| Desmidophorus sp. | 100122100112100400020230010000002 |
| Dryophthorus americanus | 100124100122100200225030021012002 |
| Stenommatus sulcifrons | 100114000122100200205030021012002 |
| Cryptoderma sp. | 100114110111100400223130000000001 |
| Orthognathus subparallelus | 100112110010100400223130000000001 |
| Mesocordylus bracteolatus | 000112210111100400203130010000002 |
| Yuccaborus frontalis | 100113010010100400223030000000001 |
| Rhinostomus thompsoni | 100112010111100400203130010000002 |
| Rhynchophorus palmarum | 100114010012000400003130000000002 |
| Otidognathus sp | 100114010012000400003130000000002 |
| Diocalandra frumenti | 100122000011000400223130011000002 |
| Toxorhinus baonii | 100114000011000400223030011000001 |
| Sitophilus oryzae | 100114000012000401023030012001002 |
| Aphiocephalus guerini | 100113010011000400223030000000002 |
| Ommatolampus paratasioides | 100114010011000400003030000012002 |
| Polytus mellerborgii | 100122000011000400223030011000002 |
| Rhodobaenus tredecimpunctatus | 100112110011000400223130000000002 |
| Scyphophorus acupunctatus | 100114010011000400003130020001002 |
| Strombocerinae gen. sp. | 100114000---000400223130022112002 |
| Notaris (Erirrhinus) festuca | 100112000122101400205130311001102 |
| Grypus leechi | 100112000011101400025130310001102 |
| Lissorhoptrus simplex | 100124100122101400005130010001002 |
| Stenopelmus rufinasus | 100124100122101400205130313001002 |
| Tanysphyrus lemnae | 100122100012100400205130013001002 |
| Tadius erirhinoides | 100122000011100400225030011000102 |
| Philacta testacea | 110122000011101400105030011001002 |
| Alaocybites sp. | --0----00---1014-0--5030022112002 |
| Gilbertiola sp. | --0----00---1014-0--5030022012002 |
| Schizomicrus caecus | --0----00---1014-0--5030022112002 |
| Perieges bardus | 100121000------420105030022111002 |

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|---|---|
| Antiquis opaque (French amber) | ???????????????2????01??1???????? |
| Curculio pardalis | 010120000033101220102131311001012 |
| Shigizo sp | 110120000133101220102130311001012 |
| Carponius axillaris | 110120000133101220102130311001012 |
| Timola sp | 110120200133101220102130311001012 |
| Acalyptus carpini | 110122000031001200102110311001012 |
| Amorphoidea lata | 110122000031001201102100311001012 |
| Acentrus histrio | 110122200031001200102130322001002 |
| Anoplus plantaris | 110122200031001200102130321001002 |
| Cionopsis lineola | 110122200011001200102130310001012 |
| Anthonomus fulvus | 110122200011001200122130310001012 |
| Camarotus sp | 100114200123101200012130323001012 |
| Odontopus calceatus | 110124200113101200022100310001012 |
| Ceratopus sp. | 110122000113101200122100311001012 |
| Cionus hortulanus | 010124000113101200000130321001012 |
| Stereonychus fraxini | 010124000113101200000130321001012 |
| Haplonyx scutellatus | 010124200113101200000100321001012 |
| Derelomus basalis | 100122000111101200102130311001012 |
| Phyllotrox (Euclyptus) sp. | 100102020131100211102130313001012 |
| Ellescus ephippiatus | 100122000113101200002130311001002 |
| Dorytomus mucidus | 100102010211101200002110011001012 |
| Sicoderus tinamus | 100114100123101200202130301000002 |
| Ludovix fasciatus | 100112100111101210202130301000002 |
| Rhopalomerus tenuirostris | 110124200113101200102130311001002 |
| Meriphus sp | 110124200111101200202130311001002 |
| Geochus tibialis | 100124200111101200202130021112002 |
| Gymnaetron tetrum | 110022200112101210122130310001002 |
| Myrmex chevrolati | 100102010233101400103130001001012 |
| Piazorhinus sp. | 110122100113101200102100312001002 |
| Pyropus cyaneus | 110123000011000200022110312001012 |
| Isochnus rufipes | 100122200111101200102130321001012 |
| Tachygonus centralis | 010101210233101420105131312011002 |
| Promecotarsus sp. | 100102200113101200002130312001012 |
| Terires sp. | 100102200113101200002130310001012 |
| Styphlus penicillus | 100102200113101200002130312001012 |
| Tychius picirostris | 100122100111101200102130312001012 |
| Lignyodes horridulus | 110120200213101100103110013001012 |
| Ulomascus parallelus | 110124010111100200222110011001012 |
| Bagous transversus | 100220200211100400125130013001012 |
| Pnigodes setosus | 100224200011100400125130013001012 |
| Hydronomus sinuatocollis | 100224110011100400205130113001012 |
| Baris torquata | 010100001011011500025101122001002 |
| Anthinobaris dispilota | 010112001111110500025101122001002 |
| Limnobaris bicincta | 010112001021010501025101121001012 |
| Torcus nigrinus | 010112001111110500005101111001012 |
| Nicentrus grossulus | 010102001111110500025101111001012 |
| Calandrinus grandicollis | 010102201111110500005130122112012 |
| Eisonyx crassipes | 010102101111110500005100122112012 |
| Pycnobaris pruinosa | 010110001011110501025101122001002 |
| Thanius sp. | 010110001011110501025101122001002 |
| Xystus ater | 110102001111110500005111110001012 |
| Madopterus talpa | 000112001011010501225131111001012 |
| Peridinetus irroratus | 000112001111110501225111110001012 |
| Barinus bivittatus | 100112001111110500025101112001012 |
| Sibariops concurrens | 000112001111110501225101110001012 |
| Diorymeropsis xanthoxyli | 000102001011010500025101121001012 |
| Mononychus punctumalbum | 000011200133110220105101111001012 |
| Pelenomus roelofsi | 000021200133110220105111123001002 |
| Rhinoncus perpendicularis | 000021200133110220105101123001002 |
| Scleropterus serratus | 000021000133110220105111113012002 |
| Rutidosoma globulus | 010021000133110220105101123012002 |
| Homorosoma asperum | 000021000133110220105101112001012 |

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|---|---|
| Amalus scortillum | 00002120013311022012510112300101 2 |
| Ceutorhynchus nitidulus | 00001120013311022010510011100101 2 |
| Cardipennis sulcithorax | 00002100013311022010510112300101 2 |
| Dieckmannius sexnotatus | 00002120013311022010510111200101 2 |
| Coeliodes rana | 00000120013311022010510111200101 2 |
| Mecysmoderes euglyptus | 00002120013311022012510112300101 2 |
| Xenysmoderodes sasajii | 00000120013311022010510112100101 2 |
| Augustinus comes | 00001120013311022010510001200101 2 |
| Auleutes epilobii | 00000120013311022010510112200101 2 |
| Cyphosenus citricola | 00002120013311022010511112200101 2 |
| Anthypurinus haloxylicola | 00002120013311022012510112300101 2 |
| Lioxyonyx fausti | 00002120013311022010510112200101 2 |
| Arachnobas gazella | 00112121013311052010511111110101 2 |
| Campyloscelus westermanni | 11102421011111050010511111100101 2 |
| Metialma straminea | 01010120113311052012510111100101 2 |
| Cyllophorus fausciatus | 00112121013311012012513111100101 2 |
| Acoptus suturalis | 10112220011111050010513111200101 2 |
| Lobotrachelus troglodytes | 01112410011311150010513111200101 2 |
| Mecopus trilineatus | 10102421001101020022511111100101 2 |
| Telephae oculata | 01012120113311052010513111100101 2 |
| Balanogastris kolae | 01012120013311052010511111000101 2 |
| Cratosomus "punctulatus" | 11000220011111022012513111100100 2 |
| Trichodocerus sp. | 10010420011311150010513111200101 2 |
| Cylindrocopturus operculatus | 01000120013311052010511111301201 2 |
| Cylindrocopturus adspersus | 01000120013311052010511112201201 2 |
| Hoplocopturus sp. | 01000120013311142010511112300101 2 |
| Cossonus impressifrons | 10012401012211040022511012300100 2 |
| Acamptus echinus | 10012220011111140020513011200100 2 |
| Araucarius sp. | 11012101023111140012503011200101 2 |
| Catolethrus sp. | 10012201011111040120503011200100 2 |
| Pseudopentarthrum atrolucens | 11112210011111040020503011300100 2 |
| Macroscytalus chisosensis | 11112210011111040020503011300100 2 |
| Proeces depressus | 11112210011111040020503011300100 2 |
| Pseudapotrepus sp. | 10012420012211050020513011200100 2 |
| Elassoptes marinus | 10112210011111040020503011201200 2 |
| Heptarthrum sp. | 01112120023111042010503002300100 2 |
| Phloeophagus minor | 11102420012211040020503011200101 2 |
| Cryptorhynchus lapathi | 01000120013311022010510011100101 2 |
| Coelosternus sp. | 11010221013311120010513111100101 2 |
| Eurhoptus sp. | 11010221013311120010513011211200 2 |
| Gerstaeckeria lecontei | 01010420013311120010513011210100 2 |
| Aedemonus erichsoni | 10010211003300120010513111200101 2 |
| Mechistocerus sp. | 11010111003110120012510111100101 2 |
| Camptorhinus sp. | 10010211013300120010513111200101 2 |
| Cophes obtenus | 00012110011310120010513111200101 2 |
| Psepholax humilis | 00010120013310122012513011100100 2 |
| Strongylopterus ovatus | 00010120013310120012513001300100 2 |
| Torneuma subpanum | 00010120013310122012523012301201 2 |
| Bronchus (Hipporhinus) bohemani | 01012020001310142012503031201200 2 |
| Amycterus elongata | 01012020001310142012503031111200 2 |
| Aegorhinus nodipennis | 01012020001310142012523031201200 2 |
| Diabathrarius sp. | 11002210011210140010523031100100 2 |
| Gonipterus gibberus | 11002010011110140002523031000100 2 |
| Emphyastes fucicola | 01012020001310142012503001201200 2 |
| Listroderes costirostris | 11012210011110140010503031100100 2 |
| Agraphus bellicus | 11012410011310142010503001311200 2 |
| Lepidophorus lineaticolllis | 110124200---10142012503001311200 2 |
| Anypotactus jansoni | 11012410011310140010203001100100 2 |
| Strophosoma melanogrammus | 11012410011310140010503001301200 2 |
| Brachyderes lusitanicus | 11012410011310140010503001311200 2 |
| Trigonops platessa | 11012410011310140010503001311200 2 |
| Cneorrhinus geminatus | 11012410011310140010203001311200 2 |

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|---|---|
| Cratopus viridisparsus | 1101221001131014001021300010010 01 |
| Cyrtepistomus castanaeus | 1101241001221014002021300000120 01 |
| Palirhoeus eatoni | 11012410012210140020503001311200 2 |
| Elytrurus griseus | 11012410012210140020503000311200 2 |
| Episomus lentus | 11012410012210140020503000111200 2 |
| Eudiagogus pulcher | 11012410011210140020523001200101 2 |
| Colecerus (Coleocerus) marmoratus | 11012410012210140020523001100100 1 |
| Eucoleocerus (Eucolecerus) sp. | 11012410012210140020523001100101 2 |
| Eupholus bennetti | 11012220011210140000213000100100 1 |
| Compsus argyreus | 11012410011210140020213000000100 2 |
| Lachnopus floridanus | 11012410011210140020213000100100 2 |
| Hormorus undulatus | 11012410011210140020213001100100 1 |
| Leparocerus morio | 11012410011210140020503001101200 2 |
| Hypoptus macularis | 11012410011210140020213001100100 1 |
| Cyrtomon (Cyphus) lautus | 11012410011210140020213001100100 2 |
| Naupactus (Graphognathus) peregrinus | 11012410011210140020203001101200 2 |
| Ophryastes (Eupagoderes) argentatus | 11012410011210140020203001211200 2 |
| Sciopithes obscurus | 11012410011210140020503001201200 2 |
| Pachyrrhynchus tobafolius | 11012410011210140020203001311200 2 |
| Stomodes gyrosicollis | 11012410011210140020503001311200 2 |
| Rhinospathe albomarginata | 11012410012210140020203000100100 1 |
| Liophloeus nubilis | 11012220011210140000203000100100 1 |
| Premnotrypes vorax | 11012410011210140020503001111200 2 |
| Prypnus scutellaris | 11012010011210140000203001100100 1 |
| Rhyncogonus gracilis | 11012410011210140000503000111200 1 |
| Mitostylus tenius | 11012010011210140000213001100100 2 |
| Sitona californicus | 11002010011110140020213001100101 1 |
| Pachnaeus litus | 11012210011210140020213001000101 1 |
| Tanyrhynchus sp. | 11012410011210140000503000111200 1 |
| Trachyphloeus aristatus | 11012410011210140000503000111200 2 |
| Rhigopsis effracta | 11012410011210140000513001311200 2 |
| Dasydema hirtella | 11012410011210140000213001201200 1 |
| Hypera punctata | 01012410011110140000303031100101 2 |
| Coniatus tamaricis | 01012410011110140000303031100101 2 |
| Tylopterus pallidus | 11012410011110140000210031100101 2 |
| Cepurellus cervinus | 11012410011110140000213031100101 2 |
| Lixus concavus | 01010121013210142012211001000101 2 |
| Larinus carlinae | 01010121013210142012211001000101 2 |
| Apleurus (Dinocleus) molitor | 11010110011100140010211001100101 2 |
| Stephanocleonus sp. | 01010110011210130010213001100101 2 |
| Rhinocyllus conicus | 11002121013100130022211031000100 2 |
| Bangasternus orientalis | 01002121013110130012211031000100 2 |
| Laemosaccus nephele | 11012210103100030022210001000101 2 |
| Neolaemosaccus (Saccolaemus) carinicollis | 11012211003100030002210001000101 2 |
| Magdallis armicollis | 11012211003100030002211001000101 2 |
| Liparus glabrirostris | 10010420011211130010513001201200 2 |
| Acicnemis sp. | 10010420011211140010501011200101 2 |
| Amorphocerus sp. | 10012400011211140022211011100101 2 |
| Rhyparonotus sp. | 10012420011211140020503001111201 2 |
| Cholus rana | 10012200011211140002211001100101 2 |
| Rhyssomatus lineaticollis | 01012420013210140010513001100101 2 |
| Cleogonus sp. | 11012012011210140022513111100101 2 |
| Conotrachelus fissunguis | 01010022011210140000513001100101 2 |
| Gononotus angulicollis | 11012022011210140020503011111200 2 |
| Guioperus trifasciatus | 11022110013310142010513001000100 2 |
| Heilus bioculatus | 11012001011211140010511001100101 2 |
| Heilipodus polygluttatus | 11012021011210140010511001100101 2 |
| Hylobius pales | 11010221011210140012513011100101 2 |
| Ithyporus stolidus | 11010222013111140010513001000100 2 |
| Sclerocardius africanus | 11012200011211140012511001100100 2 |
| Lepyrus palustris | 01012120013311142010503031200100 2 |
| Lymantes sandersoni | 01012110013311140010503001201200 2 |

| | |
|---|---|
| Alcidodes dentipes | 110122100131111400205210011001012 |
| Nettarhinus bilobus | 110220010112111400122130011001012 |
| Petalochilus gemellus | 110120010112101400102130011001012 |
| Phrynixus sp. | 110101100133101400105030012112002 |
| Pissodes strobi | 110102100133101400122130112001012 |
| Sternechus paludatus | 110120210112101300105210010001012 |
| Neophycoroetes testaceus | 110102100133101300105030112112002 |
| Trigonocolus curvipes | 000120001012101501115131021001112 |
| Trypetes sp. | 110124010112101400225110011001002 |
| Parorobitus gibbus | 000120001114101500022110011001001 |
| Scolytogenes expers | 101103220111000110203030003001102 |
| Scolytoplatypus tycon | 101113220100000110203001003001112 |
| Xyleborus spathipennis | 101113220011000110220001003001112 |
| Sphaerotrypes pila | 1011332001--000120225000003001102 |
| Alniphagus costatus | 101123000111100111225000003001012 |
| Pityophthorus jucundus | 101113200000100111225030003001112 |
| Hylurgops planirostris | 111123020000100111205030102001002 |
| Tesserocerus inermis | 111113120000000010203001000012002 |
| Scolytus multistriatus | 101113200132100310103001001000002 |
| Platypus parallelus | 101213220100000110203031011012002 |
| Ficicis despectus | 101124100122100100205000101001112 |
| Dendroctonus micans | 111123000000100110205000001001002 |
| Diapus aculeatus | 101213120100000110203031011012002 |
| Cylindrobrotus pectinatus (Lebanese amber) | 101?232001101001101000000???????? |
| Microborus inertus (Burmese amber) | ???????????????1????000?3???????? |
| indet 4 nemonychid (Yixian 2007104 1/2) | 1????3???000????1?2?0?0?0???????? |
| indet 3 nemonychid (Yixian 2010159) | 1????3???000????1?2?0?0?0???????? |
| indet 2 nemonychid (Yixian 2005111) | 1????3???000????1?2?0?0?0???????? |
| Microprobelus liuae (Yixian 2005106) | 1????3???000????1?2?0?0?0???????? |
| Microprobelus liuae (Yixian 2007102) | 1????3???000????1?2?0?0?0???????? |
| Chinocimberis augustipecteris (Yixian 2007104) | 1????3???000????1?2?000?0???????? |
| Chinocimberis augustipecteris (Yixian 2005127) | 1????3???000????1?2?000?0???????? |
| Chinocimberis magnoculi (Yixian 2010155) | 1????3???000????1?2?000?0???????? |
| Chinocimberis magnoculi (Yixian 2005107) | 1????3???000????1?2?000?0???????? |
| Chinocimberis augustipecteris (Yixian 2005102) | 1????3???000????1?2?000?0???????? |
| Renicimberis latipecteris (Yixian 2005123) | 1????3???000????1?2?000?0???????? |
| Renicimberis latipecteris (Yixian 2010153) | 1????3???000????1?2?000?0???????? |
| Renicimberis latipecteris (Yixian 2005101) | 1????3???000????1?2?000?0???????? |
| Renicimberis latipecteris (Yixian 2007101) | 1????3???000????1?2?000?0???????? |
| A. concavus (Yixian 2007105) | 1????3???010????1?2?0?0?0???????? |
| A. brachyorhinos (Yixian 2005105) | 1????3???000????1?2?0?0?0???????? |
| A. brachyorhinos (Yixian 2005119) | 1????3???000????1?2?0?0?0???????? |
| A. brachyorhinos (Yixian 2005125) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2007103) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2010151) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2010157) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2006102) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2005110 1/2) | 1????3???000????1?2?0?0?0???????? |
| Abrocarina undet. 1 (Yixian 2010154) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2010152) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2005116 1/2) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2005118) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2005117) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2005122) | 1????3???000????1?2?0?0?0???????? |
| A. relicinus (Yixian 2010160) | 1????3???000????1?2?0?0?0???????? |
| A. macilentus (Yixian 2010156) | 1????3???000????1?2?0?0?0???????? |
| Archaeorrhynchus acutirostris | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchus latitarsus | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchus paradoxopus | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchus kryzhanovskyi | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchus nikolaevi | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchus carpenteri | ?????3????00????1?2?0?0?0???????? |

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|---|---|
| Archaeorrhynchus sukatshevai | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchoides crowsoni | ?????3????00????1?2?0?0?0???????? |
| Archaeorrhynchoides arnoldii | ?????3????00????1?2?0?0?0???????? |
| Kararhynchus occiduus | ?????3????00????1?2?0?0?0???????? |
| Eobelus longipes | ?????3????00????1?2?0?0?0???????? |
| Eobelus sp. | ?????3????00????1?2?0?0?0???????? |
| Belonotaris karatavicus | ?????3????00????1?2?0?0?0???????? |
| Probelus tibialis | ?????3????00????1?2?0?0?0???????? |
| Probelus cockerelli | ?????3????00????1?2?0?0?0???????? |
| Probelus scudderi | ?????3????00????1?2?0?0?0???????? |
| Probelus longitarsus | ?????3????00????1?2?0?0?0???????? |
| Probelus curvispinus | ?????3????00????1?2?0?0?0???????? |
| Probelus handlirschi | ?????3????00????1?2?0?0?0???????? |
| Probelopsis acutiapex | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus wanatavieus | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus gratshevi | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus zherichini | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus medvedevi | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus rasnitsyni | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus rohdendorfi | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus wickhami | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus korotyaevi | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus heeri | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus martynovi | ?????3????00????1?2?0?0?0???????? |
| Arnoldibelus karatavicus | ?????3????00????1?2?0?0?0???????? |
| Nanophydes ovatus | ?????3????00????1?2?0?0?0???????? |
| Ampliceps dentitibia | ?????3????00????1?2?0?0?0???????? |
| Ampliceps furcitibia | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides progressivus | ?????3????00????1?2?0?0?0???????? |
| Karataucarodes zimmermanni | ?????3????00????1?2?0?0?0???????? |
| Scelocamptus dubius | ?????3????00????1?2?0?0?0???????? |
| Scelocamptus curvipes | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides rohdendorfi | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides brevipes | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides zherichini | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides similis | ?????3????00????1?2?0?0?0???????? |
| Belonartis lineatipunctatus | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides mongolicus | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides gurvanensis | ?????3????00????1?2?0?0?0???????? |
| Eccoptarthroides longirostris | ?????3????00????1?2?0?0?0???????? |
| Eccoptarthroides ponomarenkoi | ?????3????00????1?2?0?0?0???????? |
| Eccoptarthroides martynovi | ?????3????00????1?2?0?0?0???????? |
| Eccoptarthroides nikitskyi | ?????3????00????1?2?0?0?0???????? |
| Pseudobrenthorrhinus magnus | ?????3????00????1?2?0?0?0???????? |
| Pseudobrenthorrhinus crassicornis | ?????3????00????1?2?0?0?0???????? |
| Brenthorrhinus mirabilis | ?????3????00????1?2?0?0?0???????? |
| Gobibrenthorrhinus gigas | ?????3????00????1?2?0?0?0???????? |
| Brenthorrhinus brevirostris | ?????3????00????1?2?0?0?0???????? |
| Brenthorrhinoides mandibulatus | ?????3????00????1?2?0?0?0???????? |
| Scelocamptus tenuirostris | ?????3????00????1?2?0?0?0???????? |
| Brenthorrhinoides robustus | ?????3????00????1?2?0?0?0???????? |
| Brenthorrhinoides pubescens | ?????3????00????1?2?0?0?0???????? |
| Mongolbrenthorrhinus arnoldii | ?????3????00????1?2?0?0?0???????? |
| Mongolbrenthorrhinus pusillus | ?????3????00????1?2?0?0?0???????? |
| Mongolbrenthorrhinus flavus | ?????3????00????1?2?0?0?0???????? |
| Testudobrenthorrhinus baissiensis | ?????3????00????1?2?0?0?0???????? |
| Testudobrenthorrhinus taetricus | ?????3????00????1?2?0?0?0???????? |
| Buryatnemonyx niger | ?????3????00????1?2?0?0?0???????? |
| Buryatnemonyx tener | ?????3????00????1?2?0?0?0???????? |
| Buryatnemonyx gratshevi | ?????3????00????1?2?0?0?0???????? |
| Oxycorynoides ponomarenkoi | ?????3????00????1?2?0?0?0???????? |
| Procurculio fortipes | ?????3????00????1?2?0?0?0???????? |

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|---|---|
| Procurculio pallens | ?????3????00????1?2?0?0?0???????? |
| Megabrenthorrhinus grandis | ?????3????00????1?2?0?0?0???????? |
| Megabrenthorrhinus longicornis | ?????3????00????1?2?0?0?0???????? |
| Eccoptarthrus crassipes | ?????3????00????1?2?0?0?0???????? |
| Eccoptothorax latipennis | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus pallidirostris | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus ovatus | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus arnoldii | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus elongatus | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus rotundicollis | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus angulatus | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus major | ?????3????00????1?2?0?0?0???????? |
| Distenorrhinus antennatus | ?????3????00????1?2?0?0?0???????? |
| Paroxycorynoides elegans | ?????3????00????1?2?0?0?0???????? |
| Selengarhynchoides sharyngolensis | ?????3????00????1?2?0?0?0???????? |
| Selengarhynchus ovalis | ?????3????00????1?2?0?0?0???????? |
| Pseudonemonyx stupendus | 1????3???000????1?2?0?0?0???????? |
| Cretonemonyx minimus | 1????3???000????1?2?0?0?0???????? |
| Cretonemonyx longirostris | 1????3???000????1?2?0?0?0???????? |
| Cretonemonyx profligatus | 1????3???000????1?2?0?0?0???????? |
| Megametrioxenoides longus | ?????3????00????1?2?0?0?0???????? |
| Megametrioxenoides proelomus | ?????3????00????1?2?0?0?0???????? |
| Cretoxenoides erdeniensis | ?????3????00????1?2?0?0?0???????? |
| Chinocimberis dispersus | ?????3????00????1?2?0?0?0???????? |
| Baissimberis prodigiosus | ?????3????00????1?2?0?0?0???????? |
| Mongolocar orcinus (nemonychid) | 1????????010????1?2?0?0?0???????? |
| Karacar contractus (nemonychid) | 1????????010????1?2?0?0?0???????? |
| Baissabrenthorrhinus mirabilis | 1????????010????1?2?0?0?0???????? |
| Ulyaniana nobilis | 1????3????30????1?2?0?0?0???????? |
| Ulyaniana excellens | 1????3????30????1?2?0?0?0???????? |
| Ulyanisca dentipes | 1????3????30????1?2?0?0?0???????? |
| Slonik sibiricus | 1????3????30????1?2?000?0???????? |
| Hyperites nadezhkini | ????????????????????00??0???????? |

TABLE 5. Characters 132 - 164

| | 132  137  142  147  152  157  162 |
|---|---|
| | \|    \|    \|    \|    \|    \|    \| |
| Cucujus clavipes | 000312000210000000200000000000000 |
| Orsodacne atra childreni (Orsodacnidae) | 101312000000000000200000000000000 |
| Fidia viticida (Chrysomelidae) | 110302000110000001200000000000000 |
| Cimberis sp. | 100312000000000000200000000000000 |
| Nannomacer germaini | 000312000000000000200000000000000 |
| Mecomacer scambus | 000312000000000000200000000000000 |
| Rhynchitomacerinus kuscheli | 000312000000000000200000000000000 |
| Nemonyx lepturoides | 000312000210000000200000000000000 |
| Doydirhynchus austriacus | 100112000000000000200000000000000 |
| Lecontellus byturoides | 100102000000000000200000000000000 |
| Arra similis (Spanish amber) | ??????0????????000200000000000000 |
| indet 5 anthribid (Yixian 2005126) | ??????0????????1???00?0000000?000 |
| Trigonorhinus sp. | 000302000001000100010000000000000 |
| Anthribus nebulosus | 000300110111000100010000000000000 |
| Epicerastes sp. | 000302000001000100010000000000000 |
| Apolecta samarana | 000302000001000100010000000000000 |
| Gynandrocerus sp. | 000002100001000100010000000000000 |
| Phaenithon semigriseum | 010300210121000100310000000000010 |
| Basitropis sp. | 000002000001000100010000000000000 |
| Strabus bimaculatus | 000000010001000100010000000000010 |
| Corrhecerus sp | 000002000001000100010000000000000 |
| Straboscopus tessellatus | 100300110111000100010000000000000 |
| Euparius marmoreus | 010302000001000100010000000000000 |
| Discotenes nigrotuberculata | 010302000001000100010000000000000 |

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|---|---|
| Ischnocerus infuscatus | 000302000001000100010000000000000 |
| Dendropemon sp. | 000002000001000100010000000000000 |
| Eucorynus crassicornis | 000002000001000100010000000000000 |
| Gymnognathus sp. | 110000211121000100010000000000000 |
| Dinema filicornis | 000302000001000100010000000000000 |
| Neseonos brunneus | 000302000001000100010000000000000 |
| Mauia subnotata | 000302000001000100010000000000000 |
| Illis anna | 000302000001000100010000000000010 |
| Mecocerus sp. | 000002100001000100010000000000000 |
| Acanthothorax basalis | 000000110111000100010000000000000 |
| Phloeophilus sulcifrons | 000000110111000100010000400000000 |
| Mycetis marginicollis | 000200110111000100010000000000000 |
| Ormiscus sp. | 001300211121000100010000000000000 |
| Ozotomerus bipunctatus | 000002000001000100010000000000000 |
| Piesocorynus sellatus | 010302000001000100010000000000000 |
| Brachycorynus distentus | 000002000001000100010000000000010 |
| Goniocloeus sp. | 001300010211000100010000000000000 |
| Platyrhinus resinosus | 000300110001000100010000000000000 |
| Phoenicobiella chamaeropis | 010302000001000100010000000000000 |
| Toxonotus fascicularis | 000002000001000100010000000000000 |
| Phloeobius pallipes | 000002000001000100010000000000000 |
| Platystomos wallacei | 000002000001000100010000000000000 |
| Ptychoderes sp. | 011302000211000100010000000000000 |
| Phloeotragus polyopras | 000002000001000100010000000000000 |
| Cerambyrhynchus schoenherri | 000002000001000100010000000000000 |
| Rhinotropis superciliaris | 000000110001000100010000000000000 |
| Sintor quadrilineatus | 000000110111000100010000000000000 |
| Allandrus bifasciatus | 000300000211000100010000000000000 |
| Stenocerus sp. | 000002000001000100010000000000000 |
| Plintheria plintheroides | 000000110111000100010000000000000 |
| Trigonorhinus sticticus | 010300000001000100010000000000000 |
| Tropideres fasciatus | 001300211111000100010000000000000 |
| Acorynus pallipes | 000200110111000100010000000000000 |
| Cedus guttatus | 000300110111000100010000000000000 |
| Xenocerus ancyra | 000000110111000100010000000000000 |
| Xylinada rugicollis | 011302000211000100010000000000000 |
| Stiboderes westermanni | 000002000001000100010000000000000 |
| Exechesops bakeri | 000300110111000100010000000000000 |
| Holostilpna sp. | 000302000211000100010000000000000 |
| Choragus sayi | 000302000001000100010000000000000 |
| Euxenus jordani | 000302000001000100010000000000000 |
| Araecerus levipennis | 000300111111000100010000000000000 |
| Acaromimus americanus | 000302000001000100010000000000000 |
| Misthosima sp. | 000300110001000100010000000000000 |
| Cisanthribus sp. | 000302000001000100010000000000000 |
| Notioxenus ater | 000302000001000100010000000000000 |
| Urodon rufipes | 000302202211000100010000000000000 |
| Rhinotia sp. | 101300210120000000200000000001000 |
| Belus semipunctatus | 100300210120000000203030111001000 |
| Homalocerus lyciformis | 100302000000000000203030011011000 |
| Pachyura australis | 101302000000000000200000000000000 |
| Dicordylus marmoratus | 100302000000000000200000111010000 |
| Daohugou belid sp. | ?????2000000000000??0000111010000 |
| Montsecbelus solutus | ????????????????0??0000000000?000 |
| Car sp. | 100302000000000003400010000000000 |
| Car condensatus | 100302000000000003400010000000000 |
| Caenominurus topali | 100302000000000000100011000000000 |
| Albicar contriti (Spanish amber) | ????????????????0?100010000000000 |
| Chilecar pilgerodendri | 100302000000000000500010000000000 |
| Carodes revelatus | ????02000000000003300011011000010 |
| Baissorhynchus tarsalis | ??????0????????0???0001000000?000 |
| Paleocar princeps | ??????0????????0?????01000000?000 |

| | |
|---|---|
| Baissacar passarius | ??????0????????0?????01000000?000 |
| Cretonanophyes longirostris | ??????0????????0???0001000000?000 |
| Cretonanophyes punctatus | ???????????????0???0001001100?000 |
| C. punctatus (Yixian 2007105 1/2) | ??????0????????0???00?1000000?000 |
| C. punctatus (Yixian 2006103) | ??????0????????0???00?1000000?000 |
| C. punctatus (Yixian 2005115) | ??????0????????0???00?1000000?000 |
| C. punctatus (Yixian 2010158) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2006101) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2005113) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2005114) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2005109) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2005112) | ??????0????????0???00?1000000?000 |
| C. zherikhini (Yixian 2005103) | ??????0????????0???0001000000?000 |
| Cretonanophyes asiaticus (sp1) | ??????0????????0???0001000000?000 |
| Cretonanophyes neocomicus (sp2) | ??????0????????0???0001000000?000 |
| Jarzembowskia edmundi | ???????????????0???00?1000000?000 |
| Baissacarodes sibiricus | ??????0????????0???0001000000?000 |
| Emanrhynchus lebedevi | ??????0????????0???0001000000?000 |
| Gobicar ponomarenkoi | ??????0????????0???0001000000?000 |
| Gobicar ulugeiensis | ??????0????????0???0001000000?000 |
| Mesophyletis calhouni | ???????????????00?10001101100?100 |
| Hispanocar kseniae | ???????????????00?100?1000000?000 |
| Martinsnetoa dubia | ???????????????00??00?1000100?000 |
| Cretocar luzzii | ???????????????00?100?1000000?000 |
| Montsecanomalus zherikhini | ???????????????00?100?1000000?000 |
| Zigras cornus | ???????????????000100010300000000 |
| Zigras nudicornus | ???????????????000100010000000000 |
| Scabridus implexus | ???????????????000100011000000000 |
| Scabridus zigrasi | ???????????????000200010000000000 |
| Anchineus dolichobothris | ???????????????00?200?1100000?010 |
| Caridae 1 | ???????????????0???000?000000?000 |
| Caridae 2 | ???????????????00??000?000000?000 |
| Caridae 3 | ???????????????000?0001000000?000 |
| Preclarusbelus vanini | ????????????????0??0?00000000?0?0 |
| Arariperhinus monnei | ????????????????0??0?00000000?0?0 |
| Gratshevbelus erici | ????????????????0?400?0100000?000 |
| Proterhinus sp. | 000302000000000001010200000000000 |
| Rhopalotria bicolor | 100302000000000000210001000000010 |
| Parallocorynus bicolor | 100302000000000001210001011000010 |
| Baltocar succinicus | ???????????????000200010001 00?000 |
| Haplorhynchites aeneus | 1003002012100000206000000 1100?000 |
| Involvulus hirtus | 1003002012100000206000000 1100?000 |
| Merhynchites bicolor | 10030220121000002020000000000?000 |
| Eugnamptus punctatus | 1003000100000000206000000 1100?010 |
| Auletobius cassandrae | 100302000000000020600000000100?000 |
| Minurus testaceus | 10030000000000002060000000000?000 |
| Pseudauletes sp. | 1003002020000000206000000 1100?000 |
| Byctiscus populi | 10030220221000002060000000000?000 |
| Listrobytiscus corvinus coeruleipennis | 10030220221000002060000000000?000 |
| Deporaus glastinus | 100302202210000020610000001 00?000 |
| Pterocolus ovatus | 00030220221000002240000001100?000 |
| Homeolabus analis | 10030020221000001001200001100?000 |
| Attelabus nigripes | 10030020221000001001200021100?000 |
| Omolabus conicollis | 00030020221000001001200001100?000 |
| Euscelus dentipes | 10030220221000001001200021100?000 |
| Henicolabus octospilotus | 10030220221000001001100000000?000 |
| Lamprolabus sandacanus | 00030020221000001001200010100?000 |
| Euops quadrifasciculatus | 10030020221000001001200001100?000 |
| Pilolabus viridans | 10030020221000001001200000000?000 |
| Apoderus sp. | 10030220221000001001200001100?000 |
| Parapoderus flavoebenus | 10030220221000001001200000100?000 |
| Clitostylus badeni | 10030220221000001001200010100?000 |

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|---|---|
| Holapoderus hystrix | 100302202210000010011000111 00?000 |
| Paroplapoderus pardalis | 10030220221000001001200000000?000 |
| Cynotrachelus roelofsi | 10030220221000001001100001100?000 |
| Trachelophorus giraffa | 1003?220221000001001200000000?000 |
| Ithycerus novemboracensis | 100302000000000000010000000000110 |
| Brentus anchorago | 100012000210000010100000200000010 |
| Arrhenodes minutus | 100012000210000012600000100000010 |
| Henarrhenodes macgregori | 100012000210000012600000100000100 |
| Baryrrhynchus schroderi | 100012000210000012600000100000100 |
| Amorphocephala imitator | 100012000210000012610000000000010 |
| Antliarhinites zamiae | 100312000210000012610000000000110 |
| Cylas formicarius elegantulus | 100312000000000011310000000000110 |
| Oncodemerus sennai | 100012000210000012600000000000110 |
| Stereodermus latirostris | 000012000110000012200000000000110 |
| Cerobates sexsulcatus | 100012000210000012200000000000110 |
| Taphroderopsis oscillator | 100012000210000013600000000000110 |
| Paratrachelizus uncimanus | 100012000210000010600000000000110 |
| Miolispa robusta | 100012000210000012600000000000110 |
| Nemocephalus guatemalensis | 100012000210000010200000000000010 |
| Diuris shelfordi | 100012000210000013600000000000110 |
| Ithystenus hollandiae | 100012000110000013600000000000110 |
| Schizotrachelus bakeri | 100012000210000012600000000000110 |
| Hormocerus scrobicollis | 100012000210000012600000000000110 |
| Ulocerus sp. | 100002000210000012600000000000110 |
| Aporhina sp. | 100002200210000011010000000000000 |
| Apion longirostre | 000300010110001013010000000000210 |
| Sayapion arizona | 100302000000001011010000000000200 |
| Perapion punctinasum | 000300010110001013010000000000200 |
| Phrissotrichum tubiferum | 100300010110001013010000000000200 |
| Alocentron attenuatum | 000302000110001013010000000000200 |
| Aspidapion radiolus | 100302000110001013010000000000200 |
| Ceratapion basicorne | 000302000110001013010000000000200 |
| Omphalapion hookeri | 100302000110001013010000000000200 |
| Cybebus dimidiatus | 100002000110001013010000000000200 |
| Exapion ulicis | 100302000110001013010000000000200 |
| Ixapion herculanum | 100300010000001013010000000000200 |
| Kalcapion flavofemoratum | 000300010110001013010000000000200 |
| Melanapion minimum | 100302000000001013010000000000200 |
| Malvapion malvae | 000300010110001013010000000000210 |
| Rhopalapion longirostre | 100302000000001013010000000000210 |
| Noterapion meorrhynchum | 100302000000001013010000000000210 |
| Eutrichapion alakanum | 000300010000001013010000000000200 |
| Capapion seniculus | 100302000000001013010000000000200 |
| Stenopterapion tenue | 100302000000001013010000000000200 |
| Trichapion gracilirostre | 000302000000001013010000000000210 |
| Chrysapion auctum | 000302000000001013010000000000200 |
| Protapion apricans | 100302000000001013010000000000200 |
| Tanaos bicolor | 000002000110001013010000000000200 |
| Nanophyes canadensis | 000302000210001013010000000000210 |
| Dieckmanniellus nitidulus | 000302000210001013010000100000210 |
| Corimalia tamarisei | 000302000000001013010000100000210 |
| Allomalia quadrivirgata | 000302000000001013010000100000200 |
| Bracycerus sp. | 100100010000000021010200000000010 |
| Microcerus costalis | 100100010000000021010200000000010 |
| Episus gibbosus | 100102000000000021010200000000000 |
| Ocladius obliquesetosus | 000100010000000022010200000000010 |
| Desmidophorus sp. | 111300010000000022010200100000010 |
| Dryophthorus americanus | 000102000111000012012000000000000 |
| Stenommatus sulcifrons | 000102000000000012012010000000000 |
| Cryptoderma sp. | 110010000110000012013000000000010 |
| Orthognathus subparallelus | 011002000110000012013110000000000 |
| Mesocordylus bracteolatus | 111002000110000022012210000000000 |

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|---|---|
| Yuccaborus frontalis | 111002000110100012013110000000000 |
| Rhinostomus thompsoni | 111002000110000022012210000000000 |
| Rhynchophorus palmarum | 111002200110000122012210000000000 |
| Otidognathus sp | 111002200110000122012210000000000 |
| Diocalandra frumenti | 111102200210000012012110000000010 |
| Toxorhinus baonii | 111102200210000012013110000000000 |
| Sitophilus oryzae | 011102200110000112012210000010010 |
| Aphiocephalus guerini | 111102000110100012013110000000000 |
| Ommatolampus paratasioides | 111102000110000122012210000000000 |
| Polytus mellerborgii | 111102200111000012012110000000010 |
| Rhodobaenus tredecimpunctatus | 111302200210000012013110000000000 |
| Scyphophorus acupunctatus | 111002000110000112012210000000010 |
| Strombocerinae gen. sp. | 010102000000000012012110000000000 |
| Notaris (Erirrhinus) festuca | 011302000110000012013010000000001 |
| Grypus leechi | 0113020000000001012013010000000001 |
| Lissorhoptrus simplex | 011302000110011012012010000000011 |
| Stenopelmus rufinasus | 000102000000001012010110000000011 |
| Tanysphyrus lemnae | 001102000000001012012110000000011 |
| Tadius erirhinoides | 001202000000011012013110000000001 |
| Philacta testacea | 011112000000010012010100000000000 |
| Alaocybites sp. | 000112000000000011010110000000201 |
| Gilbertiola sp. | 000112000000000011010110000000001 |
| Schizomicrus caecus | 000112000000000011010110010100101 |
| Perieges bardus | 000112000000000012010110000100111 |
| Antiquis opaque (French amber) | ???????????????0?2010000000000000 |
| Curculio pardalis | 111202000000010022013110100000001 |
| Shigizo sp | 111202000000000022013110100000001 |
| Carponius axillaris | 111202000000000022013110100000001 |
| Timola sp | 111202000000000022013110100000001 |
| Acalyptus carpini | 111202000000000022010110000000001 |
| Amorphoidea lata | 111200110110000022010110100000001 |
| Acentrus histrio | 011102000000000022010110000000011 |
| Anoplus plantaris | 011202000000000022012110000000001 |
| Cionopsis lineola | 111202000000000022012110100000001 |
| Anthonomus fulvus | 111202000000000022013110100000001 |
| Camarotus sp | 001102000000000022011110100000111 |
| Odontopus calceatus | 111200110210000023011110100000011 |
| Ceratopus sp. | 011302000000000022010010100000011 |
| Cionus hortulanus | 001102000000000022010010100000001 |
| Stereonychus fraxini | 001102000000000022010010100000001 |
| Haplonyx scutellatus | 001102000000000022013010100000001 |
| Derelomus basalis | 011200010000000012010110000000001 |
| Phyllotrox (Euclyptus) sp. | 011202000000000012010110000000001 |
| Ellescus ephippiatus | 011302000000000012013110000000001 |
| Dorytomus mucidus | 111202000000000022013110100000001 |
| Sicoderus tinamus | 111002000000300022012110100000011 |
| Ludovix fasciatus | 111002000000300022012110100000001 |
| Rhopalomerus tenuirostris | 111302000000300022010110100000001 |
| Meriphus sp | 111302000000000022010110100000011 |
| Geochus tibialis | 001002000000000012010110000000011 |
| Gymnaetron tetrum | 111300110110000022013010100000001 |
| Myrmex chevrolati | 011302000000000022013110100000001 |
| Piazorhinus sp. | 011200110110000023012010100100011 |
| Pyropus cyaneus | 001100210110300012010010000100001 |
| Isochnus rufipes | 111102000000000012011010000000001 |
| Tachygonus centralis | 001402000000000012011110300000001 |
| Promecotarsus sp. | 011202000000000012012010100000011 |
| Terires sp. | 011202000000000012010010000000011 |
| Styphlus penicillus | 011202000000000012010010000000011 |
| Tychius picirostris | 011202000000000012010010000000011 |
| Lignyodes horridulus | 011200000000000012013110000000001 |
| Ulomascus parallelus | 111100100000000022010111100000011 |

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|---|---|
| Bagous transversus | 01140200000000001201221000000001 |
| Pnigodes setosus | 01140200000000001201221000000001 |
| Hydronomus sinuatocollis | 01120200000000001201321000000001 |
| Baris torquata | 00150120111010001201211000000011 |
| Anthinobaris dispilota | 00150120111010001201311000000001 |
| Limnobaris bicincta | 00150120111010001201211000000001 |
| Torcus nigrinus | 01150121011020001201311000000001 |
| Nicentrus grossulus | 01150120111020001201311000000001 |
| Calandrinus grandicollis | 00150200000020001201311000000001 |
| Eisonyx crassipes | 00150200011000001201011010001001 1 |
| Pycnobaris pruinosa | 00150121111020001201211000000011 |
| Thanius sp. | 00150121111010001201311000000011 |
| Xystus ater | 01150120111010001201011000001001 1 |
| Madopterus talpa | 11150121111010001201311000000011 |
| Peridinetus irroratus | 11150021121000001201311010000000 1 |
| Barinus bivittatus | 00150121011020001201311000000001 |
| Sibariops concurrens | 11150121111010001201011000000011 |
| Diorymeropsis xanthoxyli | 00150121111010001201211000001001 1 |
| Mononychus punctumalbum | 10140200021030001101011000010001 1 |
| Pelenomus roelofsi | 10140200000000001101011000000001 1 |
| Rhinoncus perpendicularis | 10140200000000001101011000000001 1 |
| Scleropterus serratus | 11140200000000001101011000000001 1 |
| Rutidosoma globulus | 11140200000000001101311010000000 1 |
| Homorosoma asperum | 10140200000000001101311010000000 1 |
| Amalus scortillum | 11140200000000001101011000000001 1 |
| Ceutorhynchus nitidulus | 10140200021030001101011010000001 1 |
| Cardipennis sulcithorax | 11140200000000001101011010000000 1 |
| Dieckmannius sexnotatus | 10140200000030001101011000000001 1 |
| Coeliodes rana | 10140200000030001101011000000001 1 |
| Mecysmoderes euglyptus | 11140200021030001101311010000000 1 |
| Xenysmoderodes sasajii | 10140200021030001101011000010001 1 |
| Augustinus comes | 10140200021030001101011010000001 1 |
| Auleutes epilobii | 10140200021030001101311000010000 1 |
| Cyphosenus citricola | 10140200021000001101011010010001 1 |
| Anthypurinus haloxylicola | 10140200021000001101011000010001 1 |
| Lioxyonyx fausti | 11140200021030001101011000010001 1 |
| Arachnobas gazella | 11140200000000001201111010000001 1 |
| Campyloscelus westermanni | 11140200021000001201111010000001 1 |
| Metialma straminea | 01120200021000001101111010010000 1 |
| Cyllophorus fausciatus | 11120210000000002101211010000001 1 |
| Acoptus suturalis | 11120200000000002201111010000000 1 |
| Lobotrachelus troglodytes | 00140200021000002201211010000000 1 |
| Mecopus trilineatus | 11120200021000002201111010000000 1 |
| Telephae oculata | 10140210011000001201111010001001 1 |
| Balanogastris kolae | 11140210000000001201211010001000 1 |
| Cratosomus "punctulatus" | 11120210000000002201211010001001 1 |
| Trichodocerus sp. | 11120200000000002201211010000000 1 |
| Cylindrocopturus operculatus | 10140200000000002101111000000000 1 |
| Cylindrocopturus adspersus | 10140200021000001101111000000000 1 |
| Hoplocopturus sp. | 10140200021000001101111010000000 1 |
| Cossonus impressifrons | 10140200000000001201101000000001 1 |
| Acamptus echinus | 11140200000000001201101000000001 1 |
| Araucarius sp. | 01140200021000001201101000000000 1 |
| Catolethrus sp. | 11140200021000001201111000000001 1 |
| Pseudopentarthrum atrolucens | 11140200000020001201111000000001 1 |
| Macroscytalus chisosensis | 11140200000000001201111000000001 1 |
| Proeces depressus | 11140200000000001201111000000001 1 |
| Pseudapotrepus sp. | 11140200000000002201111010000001 1 |
| Elassoptes marinus | 11140200000000001201111000000001 1 |
| Heptarthrum sp. | 01140200000010001101101000000001 1 |
| Phloeophagus minor | 10140200000020001201111000000001 1 |
| Cryptorhynchus lapathi | 11130200000010000201211010001000 1 |

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|---|---|
| Coelosternus sp. | 1113020000001000020120101000010011 |
| Eurhoptus sp. | 0114020000001000110121101000000011 |
| Gerstaeckeria lecontei | 1113020000001000020120100000000011 |
| Aedemonus erichsoni | 1113020000002000230121101000000011 |
| Mechistocerus sp. | 1113000100002000120111101000000001 |
| Camptorhinus sp. | 1113020000002000020121101000010011 |
| Cophes obtenus | 1113020000001000230121101000010011 |
| Psepholax humilis | 1114020000001000230121101000000011 |
| Strongylopterus ovatus | 1114020000001000120121101000000011 |
| Torneuma subpanum | 1114020000003000110121100000000011 |
| Bronchus (Hipporhinus) bohemani | 0114120000000000210100100000001011 |
| Amycterus elongata | 1114120000003000210100100000001001 |
| Aegorhinus nodipennis | 0114120000002000230100100000000011 |
| Diabathrarius sp. | 1113120000002000230120101000001011 |
| Gonipterus gibberus | 1113120000002000220100100000001011 |
| Emphyastes fucicola | 0114120000000000120101100000000011 |
| Listroderes costirostris | 1114120000002000222001100000001011 |
| Agraphus bellicus | 0014120000000100220101200000000111 |
| Lepidophorus lineaticolllis | 0113120000000000127000100000000111 |
| Anypotactus jansoni | 0110120000000100220101101000001111 |
| Strophosoma melanogrammus | 0110120000000000220101100000000111 |
| Brachyderes lusitanicus | 0110120000000000220101100001000111 |
| Trigonops platessa | 1114120000000000220101200000000111 |
| Cneorrhinus geminatus | 1110120000000000210101200000000111 |
| Cratopus viridisparsus | 0110120000000100220101102000001111 |
| Cyrtepistomus castanaeus | 1110120000000100230100101000000111 |
| Palirhoeus eatoni | 1114120000000000120101100000000111 |
| Elytrurus griseus | 1110120000000000210101200000000111 |
| Episomus lentus | 0110120000000000220101200000000111 |
| Eudiagogus pulcher | 1013121000000100230101200000001111 |
| Colecerus (Coleocerus) marmoratus | 1113021000000100230101200000001111 |
| Eucoleocerus (Eucolecerus) sp. | 0113020000000100220101200000000111 |
| Eupholus bennetti | 0110120000000000220101200000001111 |
| Compsus argyreus | 0110120000000100120101200000001111 |
| Lachnopus floridanus | 0110120000000100220101200000001111 |
| Hormorus undulatus | 0110120000000100220100100000001111 |
| Leparocerus morio | 0110120000000000220100100000000011 |
| Hypoptus macularis | 1110120000000100120100200000001011 |
| Cyrtomon (Cyphus) lautus | 0110120000000100220101200001010111 |
| Naupactus (Graphognathus) peregrinus | 0110120000000100220101200001010111 |
| Ophryastes (Eupagoderes) argentatus | 0110120000000000220101200000000011 |
| Sciopithes obscurus | 0110120000000000227001100000000011 |
| Pachyrrhynchus tobafolius | 1110120000000000220101100000001011 |
| Stomodes gyrosicollis | 1110120000000000220101101000000011 |
| Rhinospathe albomarginata | 0110120000000100220100200001010111 |
| Liophloeus nubilis | 1110120000000100220100101001010111 |
| Premnotrypes vorax | 1114120000000000220101100000000011 |
| Prypnus scutellaris | 0113120000000100220100200001010111 |
| Rhyncogonus gracilis | 0110120000000000220101100000000111 |
| Mitostylus tenius | 0110120000002000220101100000000111 |
| Sitona californicus | 0112020002100000230101100000000011 |
| Pachnaeus litus | 0110020000000100230100200000001011 |
| Tanyrhynchus sp. | 0110120000000000120101101000000111 |
| Trachyphloeus aristatus | 0110120000000000210101200001000111 |
| Rhigopsis effracta | 0110120000000100220101100000000111 |
| Dasydema hirtella | 0110120000000100220101100001011111 |
| Hypera punctata | 0113020000000100220100100000000011 |
| Coniatus tamaricis | 0113020000000100220100100000000011 |
| Tylopterus pallidus | 0113020000000100220100100001000011 |
| Cepurellus cervinus | 0113020000000100220100100000000011 |
| Lixus concavus | 0113021000000100130130100000000001 |
| Larinus carlinae | 0112021000000100130130100000000001 |

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|---|---|
| Apleurus (Dinocleus) molitor | 0113021000000100130130100000000001 |
| Stephanocleonus sp. | 0112021000000100130130100000000001 |
| Rhinocyllus conicus | 1112021000000100130130100000000001 |
| Bangasternus orientalis | 1112021000000100130130100000000001 |
| Laemosaccus nephele | 1112002112100000100110101000000011 |
| Neolaemosaccus (Saccolaemus) carinicollis | 1112002100000000130110101000000111 |
| Magdallis armicollis | 1113022111100000100120101000001111 |
| Liparus glabrirostris | 1112120000000000120130100000001011 |
| Acicnemis sp. | 0112020000000000120121101000000011 |
| Amorphocerus sp. | 0112011010000000130121100000000011 |
| Rhyparonotus sp. | 0113120000000000120131100000001001 |
| Cholus rana | 1113020000001000130120101001000011 |
| Rhyssomatus lineaticollis | 0112020000002000230130101001000001 |
| Cleogonus sp. | 1013020000001000230100101000000011 |
| Conotrachelus fissunguis | 0012020000001000230130101001000001 |
| Gononotus angulicollis | 1113120000001000120121100000000011 |
| Guioperus trifasciatus | 1113020000000000230131100000001011 |
| Heilus bioculatus | 1112020000004100130120101001000011 |
| Heilipodus polygluttatus | 1113020000004100230120101000000011 |
| Hylobius pales | 1113020002102000230120101001000001 |
| Ithyporus stolidus | 1110020000005000220120101001000011 |
| Sclerocardius africanus | 1110020002105000230120101000001011 |
| Lepyrus palustris | 0013020000002000120130100000001001 |
| Lymantes sandersoni | 0113120000000000110121100000000011 |
| Alcidodes dentipes | 1110001100000100230130101000001111 |
| Nettarhinus bilobus | 0110020000000100230120101001111111 |
| Petalochilus gemellus | 1013020000000000220120101001010111 |
| Phrynixus sp. | 0112120000000000110131100000000001 |
| Pissodes strobi | 1112020000001100130120100001000011 |
| Sternechus paludatus | 1113020000000000130130101000001011 |
| Neophycoroetes testaceus | 1111120000000000110131100000000011 |
| Trigonocolus curvipes | 1112022012105000220120101000001011 |
| Trypetes sp. | 0113020000000000130110102001000001 |
| Parorobitus gibbus | 1111022011103000220131100000000001 |
| Scolytogenes expers | 1101020002100000200101000000000000 |
| Scolytoplatypus tycon | 0101000100000000200101000000000000 |
| Xyleborus spathipennis | 1100120000000000200101000000000000 |
| Sphaerotrypes pila | 1000000101100000200101000000000000 |
| Alniphagus costatus | 1101020000000000200101000000000000 |
| Pityophthorus jucundus | 1101020000000000200111000000000000 |
| Hylurgops planirostris | 1101020000000000200111000000000000 |
| Tesserocerus inermis | 0101002100000000100011100000000000 |
| Scolytus multistriatus | 1011020001100000100111000000000100 |
| Platypus parallelus | 2101020001100000000101000000000010 |
| Ficicis despectus | 1101000101100000200101000000000010 |
| Dendroctonus micans | 1101020001100000200101000000000010 |
| Diapus aculeatus | 1101000001100000000101000000000110 |
| Cylindrobrotus pectinatus (Lebanese amber) | ??????0????000000001000000000100 |
| Microborus inertus (Burmese amber) | ??????0????000000001000000100100 |
| indet 4 nemonychid (Yixian 2007104 1/2) | ??????0????????0???00?0000000?000 |
| indet 3 nemonychid (Yixian 2010159) | ??????0????????0???00?0100000?000 |
| indet 2 nemonychid (Yixian 2005111) | ??????0????????0???00?0000000?000 |
| Microprobelus liuae (Yixian 2005106) | ??????0????????0???00?0000000?000 |
| Microprobelus liuae (Yixian 2007102) | ??????0????????0???00?0000000?000 |
| Chinocimberis augustipecteris (Yixian 2007104) | ??????0????????0???00?0000000?000 |
| Chinocimberis augustipecteris (Yixian 2005127) | ??????0????????0???00?0000000?000 |
| Chinocimberis magnoculi (Yixian 2010155) | ??????0????????0???00?0000000?000 |
| Chinocimberis magnoculi (Yixian 2005107) | ??????0????????0???00?0000000?000 |
| Chinocimberis augustipecteris (Yixian 2005102) | ??????0????????0???00?0000000?000 |
| Renicimberis latipecteris (Yixian 2005123) | ??????0????????0???00?0000000?000 |
| Renicimberis latipecteris (Yixian 2010153) | ??????0????????0???00?0000000?000 |
| Renicimberis latipecteris (Yixian 2005101) | ??????0?????0?000??0000000000?000 |

| | |
|---|---|
| Renicimberis latipecteris (Yixian 2007101) | ??????0????????0???00?0000000?000 |
| A. concavus (Yixian 2007105) | ??????0????????0???00?0000000?000 |
| A. brachyorhinos (Yixian 2005105) | ??????0????????00??0000000000?000 |
| A. brachyorhinos (Yixian 2005119) | ??????0????????0???00?0000000?000 |
| A. brachyorhinos (Yixian 2005125) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2007103) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2010151) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2010157) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2006102) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2005110 1/2) | ??????0????????00??0000000000?000 |
| Abrocarina undet. 1 (Yixian 2010154) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2010152) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2005116 1/2) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2005118) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2005117) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2005122) | ??????0????????0???00?0000000?000 |
| A. relicinus (Yixian 2010160) | ??????0????????0???00?0000000?000 |
| A. macilentus (Yixian 2010156) | ??????0????????0???00?0000000?000 |
| Archaeorrhynchus acutirostris | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus latitarsus | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus paradoxopus | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus kryzhanovskyi | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus nikolaevi | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus carpenteri | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchus sukatshevai | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchoides crowsoni | ??????0?????0?000??0000100000?000 |
| Archaeorrhynchoides arnoldii | ??????0?????0?000??0000100000?000 |
| Kararhynchus occiduus | ??????0?????0?000??0000100000?000 |
| Eobelus longipes | ??????0?????0?000??0000100000?000 |
| Eobelus sp. | ??????0?????0?000??0000100000?000 |
| Belonotaris karatavicus | ??????0?????0?000??0000100000?000 |
| Probelus tibialis | ??????0?????0?000??0000100000?000 |
| Probelus cockerelli | ??????0?????0?000??0000100000?000 |
| Probelus scudderi | ??????0?????0?000??0000100000?000 |
| Probelus longitarsus | ??????0?????0?000??0000100000?000 |
| Probelus curvispinus | ??????0?????0?000??0000100000?000 |
| Probelus handlirschi | ??????0?????0?000??0000100000?000 |
| Probelopsis acutiapex | ??????0?????0?000??0000100000?000 |
| Arnoldibelus wanatavieus | ??????0?????0?000??0000100000?000 |
| Arnoldibelus gratshevi | ??????0?????0?000??0000100000?000 |
| Arnoldibelus zherichini | ??????0?????0?000??0000100000?000 |
| Arnoldibelus medvedevi | ??????0?????0?000??0000100000?000 |
| Arnoldibelus rasnitsyni | ??????0?????0?000??0000100000?000 |
| Arnoldibelus rohdendorfi | ??????0?????0?000??0000100000?000 |
| Arnoldibelus wickhami | ??????0?????0?000??0000100000?000 |
| Arnoldibelus korotyaevi | ??????0?????0?000??0000100000?000 |
| Arnoldibelus heeri | ??????0?????0?000??0000100000?000 |
| Arnoldibelus martynovi | ??????0?????0?000??0000100000?000 |
| Arnoldibelus karatavicus | ??????0?????0?000??0000100000?000 |
| Nanophydes ovatus | ??????0?????0?000??0000000000?000 |
| Ampliceps dentitibia | ??????0?????0?000??0000100000?000 |
| Ampliceps furcitibia | ??????0?????0?000??0000100000?000 |
| Oxycorynoides progressivus | ??????0?????0?000??0000100000?000 |
| Karataucarodes zimmermanni | ??????0?????0?000??0000100000?000 |
| Scelocamptus dubius | ??????0?????0?000??0000100000?000 |
| Scelocamptus curvipes | ??????0?????0?000??0000100000?000 |
| Oxycorynoides rohdendorfi | ??????0?????0?000??0000100000?000 |
| Oxycorynoides brevipes | ??????0?????0?000??0000100000?000 |
| Oxycorynoides zherichini | ??????0?????0?000??0000100000?000 |
| Oxycorynoides similis | ??????0?????0?000??0000100000?000 |
| Belonartis lineatipunctatus | ??????0?????0?000??0000100000?000 |
| Oxycorynoides mongolicus | ??????0?????0?000??0000100000?000 |

| | |
|---|---|
| Oxycorynoides gurvanensis | ??????0?????0?000??0000100000?000 |
| Eccoptarthroides longirostris | ??????0?????0?000??0000100000?000 |
| Eccoptarthroides ponomarenkoi | ??????0?????0?000??0000100000?000 |
| Eccoptarthroides martynovi | ??????0?????0?000??0000100000?000 |
| Eccoptarthroides nikitskyi | ??????0?????0?000??0000100000?000 |
| Pseudobrenthorrhinus magnus | ??????0?????0?000??0000100000?000 |
| Pseudobrenthorrhinus crassicornis | ??????0?????0?000??0000100000?000 |
| Brenthorrhinus mirabilis | ??????0?????0?000??0000100000?000 |
| Gobibrenthorrhinus gigas | ??????0?????0?000??0000100000?000 |
| Brenthorrhinus brevirostris | ??????0?????0?000??0000100000?000 |
| Brenthorrhinoides mandibulatus | ??????0?????0?000??0000100000?000 |
| Scelocamptus tenuirostris | ??????0?????0?000??0000100000?000 |
| Brenthorrhinoides robustus | ??????0?????0?000??0000100000?000 |
| Brenthorrhinoides pubescens | ??????0?????0?000??0000100000?000 |
| Mongolbrenthorrhinus arnoldii | ??????0?????0?000??0000000000?000 |
| Mongolbrenthorrhinus pusillus | ??????0?????0?000??0000000000?000 |
| Mongolbrenthorrhinus flavus | ??????0?????0?000??0000000000?000 |
| Testudobrenthorrhinus baissiensis | ??????0?????0?000??0000000000?000 |
| Testudobrenthorrhinus taetricus | ??????0?????0?000??0000000000?000 |
| Buryatnemonyx niger | ??????0?????0?000??0000000000?000 |
| Buryatnemonyx tener | ??????0?????0?000??0000000000?000 |
| Buryatnemonyx gratshevi | ??????0?????0?000??0000000000?000 |
| Oxycorynoides ponomarenkoi | ??????0?????0?000??0000000000?000 |
| Procurculio fortipes | ??????0?????0?000??0000100000?000 |
| Procurculio pallens | ??????0?????0?000??0000100000?000 |
| Megabrenthorrhinus grandis | ??????0?????0?000??0000100000?000 |
| Megabrenthorrhinus longicornis | ??????0?????0?000??0000100000?000 |
| Eccoptarthrus crassipes | ??????0?????0?000??0000100000?000 |
| Eccoptothorax latipennis | ??????0?????0?000??0000100000?000 |
| Distenorrhinus pallidirostris | ??????0?????0?000??0000000000?000 |
| Distenorrhinus ovatus | ??????0?????0?000??0000000000?000 |
| Distenorrhinus arnoldii | ??????0?????0?000??0000000000?000 |
| Distenorrhinus elongatus | ??????0?????0?000??0000000000?000 |
| Distenorrhinus rotundicollis | ??????0?????0?000??0000100000?000 |
| Distenorrhinus angulatus | ??????0?????0?000??0000000000?000 |
| Distenorrhinus major | ??????0?????0?000??0000000000?000 |
| Distenorrhinus antennatus | ??????0?????0?000??0000000000?000 |
| Paroxycorynoides elegans | ??????0?????0?000??0000000000?000 |
| Selengarhynchoides sharyngolensis | ??????0?????0?000??0000000000?000 |
| Selengarhynchus ovalis | ??????0?????0?000??0000000000?000 |
| Pseudonemonyx stupendus | ??????0?????0?000??0000000000?000 |
| Cretonemonyx minimus | ??????0?????0?000??0000000000?000 |
| Cretonemonyx longirostris | ??????0?????0?000??0000000000?000 |
| Cretonemonyx profligatus | ??????0?????0?000??0000000000?000 |
| Megametrioxenoides longus | ??????0?????0?000??0000000000?000 |
| Megametrioxenoides proelomus | ??????0?????0?000??0000000000?000 |
| Cretoxenoides erdeniensis | ??????0?????0?000??0000000000?000 |
| Chinocimberis dispersus | ??????0?????0?000??0000000000?000 |
| Baissimberis prodigiosus | ??????0?????0?000??0000000000?000 |
| Mongolocar orcinus (nemonychid) | ??????0????????0???1300000000?000 |
| Karacar contractus (nemonychid) | ??????0????????0???1300000000?000 |
| Baissabrenthorrhinus mirabilis | ??????0????????0???1300000000?000 |
| Ulyaniana nobilis | ??????0????????0???0000000000?200 |
| Ulyaniana excellens | ??????0????????1???0000000000?200 |
| Ulyanisca dentipes | ??????0????????1???0000000000?200 |
| Slonik sibiricus | ??????0????????0???0000000000?000 |
| Hyperites nadezhkini | ??????0????????0???0000000000?010 |

TABLE 6. Characters 165 - 197

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165  170  175  180  185  190  195
|    |    |    |    |    |    |
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| | |
|---|---|
| Cucujus clavipes | 011100201000010000000100000300000 |
| Orsodacne atra childreni (Orsodacnidae) | 031310120000010000000001000300001 |
| Fidia viticida (Chrysomelidae) | 021311120000000000000110000000000 |
| Cimberis sp. | 031311200000000000000001001210001 |
| Nannomacer germaini | 011311220000000000001001001210001 |
| Mecomacer scambus | 031311220000000000000001000220000 |
| Rhynchitomacerinus kuscheli | 031311220000000000001000001221001 |
| Nemonyx lepturoides | 031311220010000001000???????????? |
| Doydirhynchus austriacus | 031311230000000001000???????????? |
| Lecontellus byturoides | 031311230000000000000???????????? |
| Arra similis (Spanish amber) | 0111002110???00?01?00???????????? |
| indet 5 anthribid (Yixian 2005126) | 01?11?21000??10?11?01???????????? |
| Trigonorhinus sp. | 030010120010101001001102112121111 |
| Anthribus nebulosus | 010000220010101011001???????????? |
| Epicerastes sp. | 010010220020101011001???????????? |
| Apolecta samarana | 010010220010101011001???????????? |
| Gynandrocerus sp. | 010010220110101011001???????????? |
| Phaenithon semigriseum | 010010220010101011001102112120101 |
| Basitropis sp. | 010010220110101011001???????????? |
| Strabus bimaculatus | 010010220110101011001???????????? |
| Corrhecerus sp | 010010220110101011001???????????? |
| Straboscopus tessellatus | 010010220110101011001???????????? |
| Euparius marmoreus | 010010220110101011001102012120101 |
| Discotenes nigrotuberculata | 010010220110101011001102012220101 |
| Ischnocerus infuscatus | 010010220110101011001???????????? |
| Dendropemon sp. | 010010220110101011001???????????? |
| Eucorynus crassicornis | 010010220110101011001???????????? |
| Gymnognathus sp. | 010010220010101001001101002220101 |
| Dinema filicornis | 010010220110101011001???????????? |
| Neseonos brunneus | 010010220110101011001???????????? |
| Mauia subnotata | 010010220110101011001???????????? |
| Illis anna | 010010220110101011001???????????? |
| Mecocerus sp. | 010010220110101001001???????????? |
| Acanthothorax basalis | 010010220110101001001???????????? |
| Phloeophilus sulcifrons | 010010220110101011001???????????? |
| Mycetis marginicollis | 010010220110101011001???????????? |
| Ormiscus sp. | 010010220010101001001000002221111 |
| Ozotomerus bipunctatus | 010010220110101011001???????????? |
| Piesocorynus sellatus | 010010220010101001001000002221101 |
| Brachycorynus distentus | 010010220110101011001???????????? |
| Goniocloeus sp. | 010010220010101001000101002221001 |
| Platyrhinus resinosus | 010010220010101011001???????????? |
| Phoenicobiella chamaeropis | 010010220010101001000101002221001 |
| Toxonotus fascicularis | 010010220020101001001???????????? |
| Phloeobius pallipes | 010010220020101011001???????????? |
| Platystomos wallacei | 010010220020101011001???????????? |
| Ptychoderes sp. | 010010220010101001000102002121001 |
| Phloeotragus polyopras | 010010220010101001001???????????? |
| Cerambyrhynchus schoenherri | 010010220010101011001???????????? |
| Rhinotropis superciliaris | 010010220010101001001???????????? |
| Sintor quadrilineatus | 010010220010101001001???????????? |
| Allandrus bifasciatus | 011010220010101001001102002221101 |
| Stenocerus sp. | 010010220010101011001???????????? |
| Plintheria plintheroides | 010010220010101011001???????????? |
| Trigonorhinus sticticus | 011010120010101001001102002221111 |
| Tropideres fasciatus | 010010120010101001001101002221001 |
| Acorynus pallipes | 010010220010101011001???????????? |
| Cedus guttatus | 010010220010101011001???????????? |
| Xenocerus ancyra | 010010220010101011001???????????? |
| Xylinada rugicollis | 010010120010101001001101002121001 |
| Stiboderes westermanni | 011000220010101011001???????????? |
| Exechesops bakeri | 010010220010101011001???????????? |

| | |
|---|---|
| Holostilpna sp. | 011010120010111001001202122221111 |
| Choragus sayi | 011010220010101011001???????????? |
| Euxenus jordani | 011010220010101011001???????????? |
| Araecerus levipennis | 010010120010101001001102002121101 |
| Acaromimus americanus | 011010220010110001000???????????? |
| Misthosima sp. | 010010220010101011001???????????? |
| Cisanthribus sp. | 011010220010110001000???????????? |
| Notioxenus ater | 011010220010101011001???????????? |
| Urodon rufipes | 011110220010110011001???????????? |
| Rhinotia sp. | 121311100010001000000100000200000 |
| Belus semipunctatus | 111311100010002000000100000200000 |
| Homalocerus lyciformis | 141211100010002000000100000200000 |
| Pachyura australis | 121311100010001000000100000200000 |
| Dicordylus marmoratus | 121311200010001000000100000200000 |
| Daohugou belid sp. | ?21311200?10?0??00?00???????????? |
| Montsecbelus solutus | ?2131?2000???0??00?00???????????? |
| Car sp. | 121311200010001010001101002200001 |
| Car condensatus | 121311200010001010001101002200001 |
| Caenominurus topali | 121311200010001000001102102221001 |
| Albicar contriti (Spanish amber) | 1213112300???0???0?0????????????? |
| Chilecar pilgerodendri | 121311200010001010001102102221001 |
| Carodes revelatus | 12131121001000?010001102002111001 |
| Baissorhynchus tarsalis | 12?31?20000??00?00?01???????????? |
| Paleocar princeps | 03?31?2?000??0??10?01???????????? |
| Baissacar passarius | 03?31?2?000??0??10?01???????????? |
| Cretonanophyes longirostris | 12131120000??00?00?01???????????? |
| Cretonanophyes punctatus | 121311200????00????01???????????? |
| C. punctatus (Yixian 2007105 1/2) | 13?31?20000??10?00?01???????????? |
| C. punctatus (Yixian 2006103) | 12?31?20000??10?00?01???????????? |
| C. punctatus (Yixian 2005115) | 12?31?20000??10?00?00???????????? |
| C. punctatus (Yixian 2010158) | 12?31?20000??10?00?00???????????? |
| C. zherikhini (Yixian 2006101) | 12?31?20000??10?00?00???????????? |
| C. zherikhini (Yixian 2005113) | 12?31?20000??10?00?01???????????? |
| C. zherikhini (Yixian 2005114) | 12?31?20000??10?00?01???????????? |
| C. zherikhini (Yixian 2005109) | 12?31?20000??10?00?00???????????? |
| C. zherikhini (Yixian 2005112) | 12?31?20000??10?00?01???????????? |
| C. zherikhini (Yixian 2005103) | 12?31?20000??00?00?00???????????? |
| Cretonanophyes asiaticus (sp1) | 1213112?000??00?00?01???????????? |
| Cretonanophyes neocomicus (sp2) | 12131120000??00?00?01???????????? |
| Jarzembowskia edmundi | 12?31?200????00?10?01?0?????????? |
| Baissacarodes sibiricus | 12?31?20000??00?00?01???????????? |
| Emanrhynchus lebedevi | 12?31?20000??00?00?01???????????? |
| Gobicar ponomarenkoi | ????1?2?000??00?10?01???????????? |
| Gobicar ulugeiensis | 12?31?20000??00?10?01???????????? |
| Mesophyletis calhouni | ?313112100???00?10?01???????????? |
| Hispanocar kseniae | ?2?31?2?00???0??10?01???????????? |
| Martinsnetoa dubia | ?3?31?2100???0??10?01???????????? |
| Cretocar luzzii | ?3?31?2000???0??00?01???????????? |
| Montsecanomalus zherikhini | ?3?31?2?00???0??10?01???????????? |
| Zigras cornus | 1313112300???0??10?01???????????? |
| Zigras nudicornus | 1313112100???0??00?01???????????? |
| Scabridus implexus | 1313112300???0??10?01???????????? |
| Scabridus zigrasi | 1313112100???0??00?01???????????? |
| Anchineus dolichobothris | ?313112100???0??10?01???????????? |
| Caridae 1 | ?3?31?200????00?10?01???????????? |
| Caridae 2 | ?3?31?2?0????00?10?01???????????? |
| Caridae 3 | ?3?31????????00?10?01???????????? |
| Preclarusbelus vanini | ?3?31?2?00???0??00?01???????????? |
| Arariperhinus monnei | ?????????????0??00?01???????????? |
| Gratshevbelus erici | 12?31?2000???0??10?01???????????? |
| Proterhinus sp. | 011111100000001001001------------ |
| Rhopalotria bicolor | 121010200000010000000002001120001 |

| | |
|---|---|
| Parallocorynus bicolor | 121010200000010000000002001120001 |
| Baltocar succinicus | 03?31?1000???00?00?01???????????? |
| Haplorhynchites aeneus | 031010120000000000001101001211101 |
| Involvulus hirtus | 031010120000000000001101001211101 |
| Merhynchites bicolor | 031010120000000000001???????????? |
| Eugnamptus punctatus | 011010120000000000001101001200001 |
| Auletobius cassandrae | 011010120000000000000100002221111 |
| Minurus testaceus | 011010120000000010001???????????? |
| Pseudauletes sp. | 011010120000000000001101000100001 |
| Byctiscus populi | 011311120101000010000???????????? |
| Listrobytiscus corvinus coeruleipennis | 011012120110000011001???????????? |
| Deporaus glastinus | 010010120000000000001100002221111 |
| Pterocolus ovatus | 011010110010000000001102002221111 |
| Homeolabus analis | 011010000000000000000101001211001 |
| Attelabus nigripes | 011010000010010001000101000220001 |
| Omolabus conicollis | 011010000000010011001???????????? |
| Euscelus dentipes | 011010000000010001001102012221001 |
| Henicolabus octospilotus | 011010000010010001000102012201001 |
| Lamprolabus sandacanus | 011010000000010011001???????????? |
| Euops quadrifasciculatus | 011010000010010001001102012221001 |
| Pilolabus viridans | 011010000010010001001100001200001 |
| Apoderus sp. | 011010000010010001001101001201001 |
| Parapoderus flavoebenus | 011010000000010001001???????????? |
| Clitostylus badeni | 011010000000010001001???????????? |
| Holapoderus hystrix | 011010000010010001001101000200001 |
| Paroplapoderus pardalis | 01101000000001000100110?????????? |
| Cynotrachelus roelofsi | 011010000010010001001101001201001 |
| Trachelophorus giraffa | 011010000000010001001???????????? |
| Ithycerus novemboracensis | 131012100020000010001100002000000 |
| Brentus anchorago | 111110100021010000001102102121011 |
| Arrhenodes minutus | 111110100021010000001102102121001 |
| Henarrhenodes macgregori | 111110100021010000001???????????? |
| Baryrrhynchus schroderi | 111110100021010000001???????????? |
| Amorphocephala imitator | 111110100021010000001102102121001 |
| Antliarhinites zamiae | 111110100010010000001002102221001 |
| Cylas formicarius elegantulus | 111110100021010000001102112121111 |
| Oncodemerus sennai | 111110100021010000001???????????? |
| Stereodermus latirostris | 111110100021010000001002112121001 |
| Cerobates sexsulcatus | 111110100021010000001???????????? |
| Taphroderopsis oscillator | 111110100021010000001???????????? |
| Paratrachelizus uncimanus | 111110100021010000001102102121101 |
| Miolispa robusta | 111110100021010000001???????????? |
| Nemocephalus guatemalensis | 111110100021010000001102102111010 |
| Diuris shelfordi | 111110100021010000001???????????? |
| Ithystenus hollandiae | 111110100021010000001???????????? |
| Schizotrachelus bakeri | 111110100021010000001???????????? |
| Hormocerus scrobicollis | 111110100021010000001???????????? |
| Ulocerus sp. | 111110100021010000001102102121001 |
| Aporhina sp. | 111010100020011000001112002211001 |
| Apion longirostre | 111110210021011010001002112111111 |
| Sayapion arizona | 111310110021011010001???????????? |
| Perapion punctinasum | 111310100021011010001002112121111 |
| Phrissotrichum tubiferum | 111310120021011010001???????????? |
| Alocentron attenuatum | 111310210021011010001002112111111 |
| Aspidapion radiolus | 111310120021011010001???????????? |
| Ceratapion basicorne | 111310210021011010001002112111111 |
| Omphalapion hookeri | 111310110021011010001???????????? |
| Cybebus dimidiatus | 121310110020011011001102112121111 |
| Exapion ulicis | 111310120021011010001???????????? |
| Ixapion herculanum | 111310110021011010001???????????? |
| Kalcapion flavofemoratum | 111310110021011011001002112111110 |
| Melanapion minimum | 111310110021011010001???????????? |

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|---|---|
| Malvapion malvae | 111310110021011011001002112111111 |
| Rhopalapion longirostre | 111310110021011010001???????????? |
| Noterapion meorrhynchum | 111310110021011010001???????????? |
| Eutrichapion alakanum | 111310110021011010001002112121111 |
| Capapion seniculus | 111310110021011010001???????????? |
| Stenopterapion tenue | 111310110021011010001???????????? |
| Trichapion gracilirostre | 111310110021011010001002112111110 |
| Chrysapion auctum | 111310210021011010001002112111111 |
| Protapion apricans | 111310110021011010001???????????? |
| Tanaos bicolor | 121312110021010010001002112111001 |
| Nanophyes canadensis | 011310000020011011001112122221111 |
| Dieckmanniellus nitidulus | 011310000020011011001112122211011 |
| Corimalia tamarisei | 031310100020011011001112122211011 |
| Allomalia quadrivirgata | 031310100020011011001112122211011 |
| Bracycerus sp. | 031300100020010000001------------ |
| Microcerus costalis | 011100100020010000001------------ |
| Episus gibbosus | 011100200021010010001???????????? |
| Ocladius obliquesetosus | 011110100010011100001------------ |
| Desmidophorus sp. | 021210100021011111001102002121111 |
| Dryophthorus americanus | 011100100020112011001------------ |
| Stenommatus sulcifrons | 011100000020011011001???????????? |
| Cryptoderma sp. | 011110100020112011001112002121111 |
| Orthognathus subparallelus | 011110100020112011001112002121111 |
| Mesocordylus bracteolatus | 011100200020111011001???????????? |
| Yuccaborus frontalis | 011110200021012111001112002121111 |
| Rhinostomus thompsoni | 011110200020111011001???????????? |
| Rhynchophorus palmarum | 011100200020112001001???????????? |
| Otidognathus sp | 011100200020112001001???????????? |
| Diocalandra frumenti | 011110100020012011001112002121111 |
| Toxorhinus baonii | 011110100020012011001112001111111 |
| Sitophilus oryzae | 011110100020111011001???????????? |
| Aphiocephalus guerini | 011110200021012111001112012121111 |
| Ommatolampus paratasioides | 011112200020112001001???????????? |
| Polytus mellerborgii | 011110100020012011001112012121111 |
| Rhodobaenus tredecimpunctatus | 011110100020012011001112001121111 |
| Scyphophorus acupunctatus | 011110200020012011001???????????? |
| Strombocerinae gen. sp. | 011110100020011011001------------ |
| Notaris (Erirrhinus) festuca | 031310100020011011001102002221111 |
| Grypus leechi | 031310100020011011001102002221111 |
| Lissorhoptrus simplex | 031310100020011011001102002221111 |
| Stenopelmus rufinasus | 011110100021011011001002112221111 |
| Tanysphyrus lemnae | 011110100021011011001002112221111 |
| Tadius erirhinoides | 011110100020011011001102002221001 |
| Philacta testacea | 011110130020010011001???????????? |
| Alaocybites sp. | 011110100010011011001------------ |
| Gilbertiola sp. | 011100100010011011001------------ |
| Schizomicrus caecus | 011100100010011011001------------ |
| Perieges bardus | 011100100010011010001------------ |
| Antiquis opaque (French amber) | 031310210???0??11?01???????????? |
| Curculio pardalis | 011110110021012011001112112121101 |
| Shigizo sp | 011112130020012011101???????????? |
| Carponius axillaris | 011112110120012011101???????????? |
| Timola sp | 011112130120012011101???????????? |
| Acalyptus carpini | 011110230010011011001???????????? |
| Amorphoidea lata | 011112230010011011001???????????? |
| Acentrus histrio | 011110100021011011101???????????? |
| Anoplus plantaris | 011100100021011011101???????????? |
| Cionopsis lineola | 011110120010011011001???????????? |
| Anthonomus fulvus | 011110120010011011001???????????? |
| Camarotus sp | 011112230010011011001???????????? |
| Odontopus calceatus | 011112230010011011001???????????? |
| Ceratopus sp. | 011212210021011011001???????????? |

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| Cionus hortulanus | 011112000020011011001???????????? |
| Stereonychus fraxini | 011112000020011011001???????????? |
| Haplonyx scutellatus | 011212000020011011101???????????? |
| Derelomus basalis | 011110210011011011001???????????? |
| Phyllotrox (Euclyptus) sp. | 011110230010011011001???????????? |
| Ellescus ephippiatus | 011110230020011011001???????????? |
| Dorytomus mucidus | 011110100021012011001112112121001 |
| Sicoderus tinamus | 011110120020011110101???????????? |
| Ludovix fasciatus | 011110120020011110001???????????? |
| Rhopalomerus tenuirostris | 011310230010011111101???????????? |
| Meriphus sp | 011310230010011011101???????????? |
| Geochus tibialis | 021200100010011011001???????????? |
| Gymnaetron tetrum | 011110000110012011001???????????? |
| Myrmex chevrolati | 011110110010012010101112112121101 |
| Piazorhinus sp. | 011110210110011010001???????????? |
| Pyropus cyaneus | 031212220020012111001???????????? |
| Isochnus rufipes | 011111210010011011001???????????? |
| Tachygonus centralis | 011110110010012011001212112221111 |
| Promecotarsus sp. | 011110100010011011001???????????? |
| Terires sp. | 011110100010011011001???????????? |
| Styphlus penicillus | 011110100010011011001???????????? |
| Tychius picirostris | 011110120010011011101???????????? |
| Lignyodes horridulus | 011110120010012011001112112221101 |
| Ulomascus parallelus | 011112230010011010001???????????? |
| Bagous transversus | 011100100020012011101112112221111 |
| Pnigodes setosus | 011100100020012011101112112221111 |
| Hydronomus sinuatocollis | 011100100020012011101112112221111 |
| Baris torquata | 011110000021012111001112112221101 |
| Anthinobaris dispilota | 011110000020011111001???????????? |
| Limnobaris bicincta | 011110100021011101001???????????? |
| Torcus nigrinus | 011112100021011101001???????????? |
| Nicentrus grossulus | 011112130121011101001???????????? |
| Calandrinus grandicollis | 011110100021011111001???????????? |
| Eisonyx crassipes | 111110000021011011001???????????? |
| Pycnobaris pruinosa | 011110100021012111001112112221101 |
| Thanius sp. | 011110000021012111001112112221101 |
| Xystus ater | 111112100121011101001???????????? |
| Madopterus talpa | 111312100121011101001???????????? |
| Peridinetus irroratus | 111312100120011011101???????????? |
| Barinus bivittatus | 111212000021011101001???????????? |
| Sibariops concurrens | 111310100021011101001???????????? |
| Diorymeropsis xanthoxyli | 111310100121011101001???????????? |
| Mononychus punctumalbum | 011110120120012111001112112221001 |
| Pelenomus roelofsi | 011110120120012011101???????????? |
| Rhinoncus perpendicularis | 011110120120012011101???????????? |
| Scleropterus serratus | 011110120010012011101???????????? |
| Rutidosoma globulus | 011110120020012011101???????????? |
| Homorosoma asperum | 011110120120012011101???????????? |
| Amalus scortillum | 011110120020011011101???????????? |
| Ceutorhynchus nitidulus | 011110120120012111001112112221001 |
| Cardipennis sulcithorax | 011110120120012011101???????????? |
| Dieckmannius sexnotatus | 011110120020012111101???????????? |
| Coeliodes rana | 011110120020012111101???????????? |
| Mecysmoderes euglyptus | 111110100020012111101???????????? |
| Xenysmoderodes sasajii | 111110120020012111101???????????? |
| Augustinus comes | 011110120020012111001112112221001 |
| Auleutes epilobii | 011110120020012111101???????????? |
| Cyphosenus citricola | 111110120020012011101???????????? |
| Anthypurinus haloxylicola | 011110100020012011101???????????? |
| Lioxyonyx fausti | 011110120020012111101???????????? |
| Arachnobas gazella | 031212100021012011001???????????? |
| Campyloscelus westermanni | 011110100020012011101???????????? |

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| Metialma straminea | 011110100021012011001112112221101 |
| Cyllophorus fausciatus | 011110100021012011001???????????? |
| Acoptus suturalis | 011110100120011011101???????????? |
| Lobotrachelus troglodytes | 011112110021012011001???????????? |
| Mecopus trilineatus | 011110100020012011001112112221101 |
| Telephae oculata | 011110110121012011001???????????? |
| Balanogastris kolae | 011110100021011001001???????????? |
| Cratosomus "punctulatus" | 011212100021012001001???????????? |
| Trichodocerus sp. | 011110230021012011001???????????? |
| Cylindrocopturus operculatus | 011110230121011011001???????????? |
| Cylindrocopturus adspersus | 011110100121012011001212112221111 |
| Hoplocopturus sp. | 011110100121012011001???????????? |
| Cossonus impressifrons | 011110100010012011001212112221111 |
| Acamptus echinus | 011100100120012011001???????????? |
| Araucarius sp. | 011110100010012011001112112221101 |
| Catolethrus sp. | 011100100020011011101???????????? |
| Pseudopentarthrum atrolucens | 011110100020011111101???????????? |
| Macroscytalus chisosensis | 011110100010011011101???????????? |
| Proeces depressus | 011110100010011011101???????????? |
| Pseudapotrepus sp. | 011100100020011011101???????????? |
| Elassoptes marinus | 011100100010011011001???????????? |
| Heptarthrum sp. | 011100100010011111001------------ |
| Phloeophagus minor | 011100100020011111101???????????? |
| Cryptorhynchus lapathi | 031312100121012111101112112221001 |
| Coelosternus sp. | 031310100121012111101???????????? |
| Eurhoptus sp. | 011110100010011111101???????????? |
| Gerstaeckeria lecontei | 011110100020012111101???????????? |
| Aedemonus erichsoni | 011110100021012111101???????????? |
| Mechistocerus sp. | 031310100021012111101112112221001 |
| Camptorhinus sp. | 011110100020012111101???????????? |
| Cophes obtenus | 011110100021012111101???????????? |
| Psepholax humilis | 011110100021012111101???????????? |
| Strongylopterus ovatus | 0311101000200121110011----------- |
| Torneuma subpanum | 011110100021012111101???????????? |
| Bronchus (Hipporhinus) bohemani | 031210100010011010001------------ |
| Amycterus elongata | 131210100010011110001???????????? |
| Aegorhinus nodipennis | 031210100121011110001102102221101 |
| Diabathrarius sp. | 031202100021011110101???????????? |
| Gonipterus gibberus | 031212100121011110101???????????? |
| Emphyastes fucicola | 031110100110011010001------------ |
| Listroderes costirostris | 011110100021011110101???????????? |
| Agraphus bellicus | 011310100111111010101???????????? |
| Lepidophorus lineaticolllis | 031310100110111010001------------ |
| Anypotactus jansoni | 031312000020111010101???????????? |
| Strophosoma melanogrammus | 031312000010111010001???????????? |
| Brachyderes lusitanicus | 031312000110111010001???????????? |
| Trigonops platessa | 031312100110112010001???????????? |
| Cneorrhinus geminatus | 031310000010111010001???????????? |
| Cratopus viridisparsus | 031312000011111010101???????????? |
| Cyrtepistomus castanaeus | 011310100010111010101???????????? |
| Palirhoeus eatoni | 011310100000110000001???????????? |
| Elytrurus griseus | 031312000010112011001???????????? |
| Episomus lentus | 031312000020112011101???????????? |
| Eudiagogus pulcher | 031312100120112011101???????????? |
| Colecerus (Coleocerus) marmoratus | 031312100120111011101???????????? |
| Eucoleocerus (Eucolecerus) sp. | 031312000020111011101???????????? |
| Eupholus bennetti | 031212100121112010101???????????? |
| Compsus argyreus | 031312100121112010111101002101101 |
| Lachnopus floridanus | 031312100121112011111------------ |
| Hormorus undulatus | 031312100021112011101???????????? |
| Leparocerus morio | 011310000111111010111???????????? |
| Hypoptus macularis | 031310100111111010111???????????? |

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| Cyrtomon (Cyphus) lautus | 021212100121111010111???????????? |
| Naupactus (Graphognathus) peregrinus | 031310100111111011101???????????? |
| Ophryastes (Eupagoderes) argentatus | 031310100011111010111???????????? |
| Sciopithes obscurus | 031310100010011010011???????????? |
| Pachyrrhynchus tobafolius | 031312100011111011101???????????? |
| Stomodes gyrosicollis | 031312100110111010011???????????? |
| Rhinospathe albomarginata | 031212100021112010101???????????? |
| Liophloeus nubilis | 011312000010111010111???????????? |
| Premnotrypes vorax | 011312100111110010111???????????? |
| Prypnus scutellaris | 031312100021111011101???????????? |
| Rhyncogonus gracilis | 031312100010110000100???????????? |
| Mitostylus tenius | 011110000021111110101???????????? |
| Sitona californicus | 031310100121111011101101002121101 |
| Pachnaeus litus | 021212100021112011101???????????? |
| Tanyrhynchus sp. | 031310100010111001111???????????? |
| Trachyphloeus aristatus | 031310100010111011111???????????? |
| Rhigopsis effracta | 031310100021112011111???????????? |
| Dasydema hirtella | 011312100011111011111???????????? |
| Hypera punctata | 031112100121012011101102002121001 |
| Coniatus tamaricis | 031310100120012011101102012121111 |
| Tylopterus pallidus | 031310120020012011101102002121111 |
| Cepurellus cervinus | 031312100021112011101???????????? |
| Lixus concavus | 031312000020012010101112002121010 |
| Larinus carlinae | 031312000020012010101102002121010 |
| Apleurus (Dinocleus) molitor | 031310000020012010101112002121000 |
| Stephanocleonus sp. | 011310000020012010101???????????? |
| Rhinocyllus conicus | 011312000020012010101112002121000 |
| Bangasternus orientalis | 011312000120012010101???????????? |
| Laemosaccus nephele | 011310100020012011001112102121101 |
| Neolaemosaccus (Saccolaemus) carinicollis | 011312200020012011001112102121101 |
| Magdallis armicollis | 011310110020012011001112112121001 |
| Liparus glabrirostris | 031312100021011000001???????????? |
| Acicnemis sp. | 011110100021011010101???????????? |
| Amorphocerus sp. | 011112100021011011101???????????? |
| Rhyparonotus sp. | 011312100020012011101???????????? |
| Cholus rana | 031212100120012110101???????????? |
| Rhyssomatus lineaticollis | 011110120021012111101112112121001 |
| Cleogonus sp. | 011312100021012110101???????????? |
| Conotrachelus fissunguis | 011112120021012111001112102121001 |
| Gononotus angulicollis | 011310100020012111101???????????? |
| Guioperus trifasciatus | 031212000021012010101???????????? |
| Heilus bioculatus | 031312100121012111101???????????? |
| Heilipodus polygluttatus | 031312100121012111101???????????? |
| Hylobius pales | 031310100121012111101???????????? |
| Ithyporus stolidus | 031310100021012111101112002121111 |
| Sclerocardius africanus | 011310100021012111101???????????? |
| Lepyrus palustris | 011310100121012111101???????????? |
| Lymantes sandersoni | 011100100020012011101???????????? |
| Alcidodes dentipes | 031212120020012010101???????????? |
| Nettarhinus bilobus | 031212100021012011101???????????? |
| Petalochilus gemellus | 031312100021012011101???????????? |
| Phrynixus sp. | 011100100011012010101???????????? |
| Pissodes strobi | 011312100021011111101???????????? |
| Sternechus paludatus | 031312000121012011101???????????? |
| Neophycoroetes testaceus | 011312100020011011101???????????? |
| Trigonocolus curvipes | 011310100120012100101???????????? |
| Trypetes sp. | 031312100021012001101???????????? |
| Parorobitus gibbus | 011112020020012111001???????????? |
| Scolytogenes expers | 011110100010011011011212112121111 |
| Scolytoplatypus tycon | 011100100010011011011012112121111 |
| Xyleborus spathipennis | 011100100010011011011012112121111 |
| Sphaerotrypes pila | 011110100010011011011012112121111 |

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|---|---|
| Alniphagus costatus | 011110100010011011011112112121111 |
| Pityophthorus jucundus | 011100100000010011011212112121111 |
| Hylurgops planirostris | 011110100010011011011112112121101 |
| Tesserocerus inermis | 010100100010011011011102112121111 |
| Scolytus multistriatus | 011100100010011011011112112121111 |
| Platypus parallelus | 010100200000011011111112012121111 |
| Ficicis despectus | 011110200010011011011212112121111 |
| Dendroctonus micans | 011110200010011011011212112121111 |
| Diapus aculeatus | 010100201010010011111112012121111 |
| Cylindrobrotus pectinatus (Lebanese amber) | 011100200010001011001???????????? |
| Microborus inertus (Burmese amber) | 011100200010001011011???????????? |
| indet 4 nemonychid (Yixian 2007104 1/2) | 0313112100??00?00?00????????????? |
| indet 3 nemonychid (Yixian 2010159) | 0010112100??00?00?00????????????? |
| indet 2 nemonychid (Yixian 2005111) | 0313112100??00?00?01????????????? |
| Microprobelus liuae (Yixian 2005106) | 0010112100??00?00?00????????????? |
| Microprobelus liuae (Yixian 2007102) | 0010112100??00?00?00????????????? |
| Chinocimberis augustipecteris (Yixian 2007104) | 0313112100??00?00?00????????????? |
| Chinocimberis augustipecteris (Yixian 2005127) | 0313112100??00?00?00????????????? |
| Chinocimberis magnoculi (Yixian 2010155) | 0313112100??00?00?00????????????? |
| Chinocimberis magnoculi (Yixian 2005107) | 0313112100??00?00?00????????????? |
| Chinocimberis augustipecteris (Yixian 2005102) | 0313112100??00?00?00????????????? |
| Renicimberis latipecteris (Yixian 2005123) | 0313112100??00?00?00????????????? |
| Renicimberis latipecteris (Yixian 2010153) | 0313112100??00?00?00????????????? |
| Renicimberis latipecteris (Yixian 2005101) | 0313112100??00000?00????????????? |
| Renicimberis latipecteris (Yixian 2007101) | 0313112100??00?00?01????????????? |
| A. concavus (Yixian 2007105) | 1213112000??10?00?01????????????? |
| A. brachyorhinos (Yixian 2005105) | 0313112100??00?10?01????????????? |
| A. brachyorhinos (Yixian 2005119) | 0111112100??10?10?01????????????? |
| A. brachyorhinos (Yixian 2005125) | 0313112000??10?10?01????????????? |
| A. macilentus (Yixian 2007103) | 0111112100??10?10?01????????????? |
| A. macilentus (Yixian 2010151) | 0313112000??10?10?01????????????? |
| A. macilentus (Yixian 2010157) | 0313112000??10?10?01????????????? |
| A. macilentus (Yixian 2006102) | 0313112000??10?10?01????????????? |
| A. macilentus (Yixian 2005110 1/2) | 0313112100??00?10?01????????????? |
| Abrocarina undet. 1 (Yixian 2010154) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2010152) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2005116 1/2) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2005118) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2005117) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2005122) | 0313112000??10?10?01????????????? |
| A. relicinus (Yixian 2010160) | 0313112000??10?10?01????????????? |
| A. macilentus (Yixian 2010156) | 0313112000??10?10?01????????????? |
| Archaeorrhynchus acutirostris | 0412112200???1?000?00???????????? |
| Archaeorrhynchus latitarsus | 0412112200???1?000?00???????????? |
| Archaeorrhynchus paradoxopus | 0412112200???1?000?00???????????? |
| Archaeorrhynchus kryzhanovskyi | 0412112200???1?000?00???????????? |
| Archaeorrhynchus nikolaevi | 0412112200???1?000?00???????????? |
| Archaeorrhynchus carpenteri | 0412112200???1?000?00???????????? |
| Archaeorrhynchus sukatshevai | 0412112200???1?000?00???????????? |
| Archaeorrhynchoides crowsoni | 0412112200???1?000?00???????????? |
| Archaeorrhynchoides arnoldii | 0412112200???1?000?00???????????? |
| Kararhynchus occiduus | 0412112200???1?000?00???????????? |
| Eobelus longipes | 0412112200???1?000?00???????????? |
| Eobelus sp. | 0412112200???1?000?00???????????? |
| Belonotaris karatavicus | 0412112200???1?000?00???????????? |
| Probelus tibialis | 0412112200???1?000?00???????????? |
| Probelus cockerelli | 0412112200???1?000?00???????????? |
| Probelus scudderi | 0412112200???1?000?00???????????? |
| Probelus longitarsus | 0412112200???1?000?00???????????? |
| Probelus curvispinus | 0412112200???1?000?00???????????? |
| Probelus handlirschi | 0412112200???1?000?00???????????? |
| Probelopsis acutiapex | 0412112200???1?000?00???????????? |

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| Arnoldibelus wanatavieus | 0412112200???1?000?00???????????? |
| Arnoldibelus gratshevi | 0412112200???1?000?00???????????? |
| Arnoldibelus zherichini | 0412112200???1?000?00???????????? |
| Arnoldibelus medvedevi | 0412112200???1?000?00???????????? |
| Arnoldibelus rasnitsyni | 0412112200???1?000?00???????????? |
| Arnoldibelus rohdendorfi | 0412112200???1?000?00???????????? |
| Arnoldibelus wickhami | 0412112200???1?000?00???????????? |
| Arnoldibelus korotyaevi | 0412112200???1?000?00???????????? |
| Arnoldibelus heeri | 0412112200???1?000?00???????????? |
| Arnoldibelus martynovi | 0412112200???1?000?00???????????? |
| Arnoldibelus karatavicus | 0412112200???1?000?00???????????? |
| Nanophydes ovatus | 0313112200???1?000?00???????????? |
| Ampliceps dentitibia | 0213112?00???1?000?00???????????? |
| Ampliceps furcitibia | 0213112?00???1?000?00???????????? |
| Oxycorynoides progressivus | 0213112?00???1?000?00???????????? |
| Karataucarodes zimmermanni | 0213112?00???1?000?00???????????? |
| Scelocamptus dubius | 0213112?00???1?000?00???????????? |
| Scelocamptus curvipes | 0213112?00???1?000?00???????????? |
| Oxycorynoides rohdendorfi | 0213112?00???1?000?00???????????? |
| Oxycorynoides brevipes | 0213112?00???1?000?00???????????? |
| Oxycorynoides zherichini | 0213112?00???1?000?00???????????? |
| Oxycorynoides similis | 0213112?00???1?000?00???????????? |
| Belonartis lineatipunctatus | 0213112?00???1?000?00???????????? |
| Oxycorynoides mongolicus | 0213112?00???1?000?00???????????? |
| Oxycorynoides gurvanensis | 0213112?00???1?000?00???????????? |
| Eccoptarthroides longirostris | 0412112200???1?000?00???????????? |
| Eccoptarthroides ponomarenkoi | 0412112200???1?000?00???????????? |
| Eccoptarthroides martynovi | 0412112200???1?000?00???????????? |
| Eccoptarthroides nikitskyi | 0412112200???1?000?00???????????? |
| Pseudobrenthorrhinus magnus | 0412112200???1?000?00???????????? |
| Pseudobrenthorrhinus crassicornis | 0412112200???1?000?00???????????? |
| Brenthorrhinus mirabilis | 0212112?000??00000?00???????????? |
| Gobibrenthorrhinus gigas | 0412112200???10000?00???????????? |
| Brenthorrhinus brevirostris | 0412112200???10000?00???????????? |
| Brenthorrhinoides mandibulatus | 0412112200???10000?00???????????? |
| Scelocamptus tenuirostris | 0412112200???10000?00???????????? |
| Brenthorrhinoides robustus | 0412112200???10000?00???????????? |
| Brenthorrhinoides pubescens | 0412112200???10000?00???????????? |
| Mongolbrenthorrhinus arnoldii | 0010112?00???10000?01???????????? |
| Mongolbrenthorrhinus pusillus | 0010112?00???10000?01???????????? |
| Mongolbrenthorrhinus flavus | 0010112?00???10000?01???????????? |
| Testudobrenthorrhinus baissiensis | 0010112?00???10000?01???????????? |
| Testudobrenthorrhinus taetricus | 0010112?00???10000?01???????????? |
| Buryatnemonyx niger | 0010112?00???10000?01???????????? |
| Buryatnemonyx tener | 0010112?00???10000?01???????????? |
| Buryatnemonyx gratshevi | 0010112?00???10000?01???????????? |
| Oxycorynoides ponomarenkoi | 0010112?00???00000?00???????????? |
| Procurculio fortipes | 0010112?00???00000?00???????????? |
| Procurculio pallens | 0010112?00???00000?00???????????? |
| Megabrenthorrhinus grandis | 0010112?00???00000?00???????????? |
| Megabrenthorrhinus longicornis | 0010112?00???00000?00???????????? |
| Eccoptarthrus crassipes | 0010112?00???00000?00???????????? |
| Eccoptothorax latipennis | 0010112?00???00000?00???????????? |
| Distenorrhinus pallidirostris | 0010112?00???00000?00???????????? |
| Distenorrhinus ovatus | 0010112?00???00000?00???????????? |
| Distenorrhinus arnoldii | 0010112?00???00000?00???????????? |
| Distenorrhinus elongatus | 0010112?00???00000?00???????????? |
| Distenorrhinus rotundicollis | 0010112?00???00000?00???????????? |
| Distenorrhinus angulatus | 0010112?00???00000?00???????????? |
| Distenorrhinus major | 0010112?00???00000?00???????????? |
| Distenorrhinus antennatus | 0010112?00???00000?00???????????? |
| Paroxycorynoides elegans | 0010112?00???00000?00???????????? |

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|---|---|
| Selengarhynchoides sharyngolensis | 0010112?00???00000?00???????????? |
| Selengarhynchus ovalis | 0010112?00???00000?00???????????? |
| Pseudonemonyx stupendus | 0?1?1121000??00000?00???????????? |
| Cretonemonyx minimus | 0?1?1121000??00000?00???????????? |
| Cretonemonyx longirostris | 0?1?1121000??00000?00???????????? |
| Cretonemonyx profligatus | 0?1?1121000??00000?00???????????? |
| Megametrioxenoides longus | 0010112?00???00000?00???????????? |
| Megametrioxenoides proelomus | 0010112?00???00000?00???????????? |
| Cretoxenoides erdeniensis | 0010112?00???00000?00???????????? |
| Chinocimberis dispersus | 0010112?00???10010?00???????????? |
| Baissimberis prodigiosus | 0010112?00???10010?00???????????? |
| Mongolocar orcinus (nemonychid) | 0313112?000??0??10?01???????????? |
| Karacar contractus (nemonychid) | 0313112?000??0??10?01???????????? |
| Baissabrenthorrhinus mirabilis | 0313112?000??0??10?01???????????? |
| Ulyaniana nobilis | 031311??00???0??00?00???????????? |
| Ulyaniana excellens | 031311??00???0??00?00???????????? |
| Ulyanisca dentipes | 031311??00???0??00?00???????????? |
| Slonik sibiricus | 0313112?00???0??01?01???????????? |
| Hyperites nadezhkini | 0313121000???0??11?01???????????? |

TABLE 7. Characters 198 - 230

| | 198 203 208 213 218 223 228 |
|---|---|
| Cucujus clavipes | 001004000001120101010101000000110 |
| Orsodacne atra childreni (Orsodacnidae) | 001003001001101101000101000100110 |
| Fidia viticida (Chrysomelidae) | 001010002021120101010101000000110 |
| Cimberis sp. | 101002000001101101000101000100110 |
| Nannomacer germaini | 101002000001101101000101000100110 |
| Mecomacer scambus | 101004000001101011000101000100110 |
| Rhynchitomacerinus kuscheli | 101004000001101011000101000100110 |
| Nemonyx lepturoides | ??1003001211101100000101000000110 |
| Doydirhynchus austriacus | ??1003000211101101000101000100110 |
| Lecontellus byturoides | ??1003001111101011000101000100110 |
| Arra similis (Spanish amber) | ??????????????????????????????110 |
| indet 5 anthribid (Yixian 2005126) | ????????????????????????????????? |
| Trigonorhinus sp. | 110102100111102211210001000030110 |
| Anthribus nebulosus | ??0104101111102211110001000030110 |
| Epicerastes sp. | ??0104101111112211011001000030100 |
| Apolecta samarana | ??0104101111102210211001000020100 |
| Gynandrocerus sp. | ??0104100111102211211001000000110 |
| Phaenithon semigriseum | 110102100111112211210001000000300 |
| Basitropis sp. | ??0104100111112211211001000000111 |
| Strabus bimaculatus | ??0104100111012211111001000200111 |
| Corrhecerus sp | ??0104101111112211201001000000111 |
| Straboscopus tessellatus | ??0104001111012211111001000000101 |
| Euparius marmoreus | 110104100111112211210001000030301 |
| Discotenes nigrotuberculata | 110104101111112211210001000000111 |
| Ischnocerus infuscatus | ??0104100111112211211001000230100 |
| Dendropemon sp. | ??0104100111112211211001000230110 |
| Eucorynus crassicornis | ??0104100111112211211001000230110 |
| Gymnognathus sp. | 110102101111112211210001001000300 |
| Dinema filicornis | ??0104100111112211211001000230101 |
| Neseonos brunneus | ??0104100111112211111001000230101 |
| Mauia subnotata | ??0104100111112211011001000230101 |
| Illis anna | ??0104100111102211011001000230311 |
| Mecocerus sp. | ??0104000111112211111001000200301 |
| Acanthothorax basalis | ??0104000111112211111001000200301 |
| Phloeophilus sulcifrons | ??0104100111112211211001000200301 |
| Mycetis marginicollis | ??0104100111112210011001000200101 |
| Ormiscus sp. | 110105101111012111010001001000310 |
| Ozotomerus bipunctatus | ??0104100111112011211001000200111 |

| | |
|---|---|
| Piesocorynus sellatus | 100102101111012111010001001000110 |
| Brachycorynus distentus | ??0104100111102011011001000200110 |
| Goniocloeus sp. | 100104101111012111010001001000110 |
| Platyrhinus resinosus | ??0104001111012210111001000000100 |
| Phoenicobiella chamaeropis | 100104101111112011210001001100110 |
| Toxonotus fascicularis | ??0104101111112011111001000100310 |
| Phloeobius pallipes | ??0104101111112211211001000000310 |
| Platystomos wallacei | ??0104101111112211211001000000310 |
| Ptychoderes sp. | 100104101111112011200001001100310 |
| Phloeotragus polyopras | ??0104101111112211211001000130110 |
| Cerambyrhynchus schoenherri | ??0104101111112011211001000130110 |
| Rhinotropis superciliaris | ??0104101111112211111101000100110 |
| Sintor quadrilineatus | ??0104101111112211211001000100110 |
| Allandrus bifasciatus | 100104101111112011200001001200110 |
| Stenocerus sp. | ??0104101111112011200001000000111 |
| Plintheria plintheroides | ??0104101111112011011001000100111 |
| Trigonorhinus sticticus | 111102101111112011010001001200110 |
| Tropideres fasciatus | 111102101101112011010001001200111 |
| Acorynus pallipes | ??0102100100102211111001000000111 |
| Cedus guttatus | ??0102101100102211001001000000111 |
| Xenocerus ancyra | ??0102101111102011011001000000110 |
| Xylinada rugicollis | 110102101111102011010001001200110 |
| Stiboderes westermanni | ??0102101111102011011001000000110 |
| Exechesops bakeri | ??0102101111112011011001001200110 |
| Holostilpna sp. | 111102101111112011010001000210110 |
| Choragus sayi | ??0102101111112211011001000230110 |
| Euxenus jordani | ??0102001111112211011001000130110 |
| Araecerus levipennis | 110102101111112011010001000210110 |
| Acaromimus americanus | ??0102001111112211011001000000110 |
| Misthosima sp. | ??0102101111112211111001000000111 |
| Cisanthribus sp. | ??0102101111102211211001000000110 |
| Notioxenus ater | ??0102101111102211011001000130111 |
| Urodon rufipes | ??0102101211002010210001000000110 |
| Rhinotia sp. | 001002001211101000010101111000002 |
| Belus semipunctatus | 001002001011101000000101110200002 |
| Homalocerus lyciformis | 001002001011101000000101110200002 |
| Pachyura australis | 000002001211101000000101111200002 |
| Dicordylus marmoratus | 001002001211101010000101110200002 |
| Daohugou belid sp. | ??????????????????????????????002 |
| Montsecbelus solutus | ????????????????????????????????? |
| Car sp. | 101004100211101011000100211100110 |
| Car condensatus | 101004000211101101000100211100110 |
| Caenominurus topali | 101014010111101001001100211200110 |
| Albicar contriti (Spanish amber) | ??????????????????????????????110 |
| Chilecar pilgerodendri | 101014010111101001000100211100110 |
| Carodes revelatus | 10?013010111101001000?????????310 |
| Baissorhynchus tarsalis | ??????????????????????????????110 |
| Paleocar princeps | ??????????????????????????????110 |
| Baissacar passarius | ??????????????????????????????110 |
| Cretonanophyes longirostris | ??????????????????????????????110 |
| Cretonanophyes punctatus | ??????????????????????????????110 |
| C. punctatus (Yixian 2007105 1/2) | ????????????????????????????????? |
| C. punctatus (Yixian 2006103) | ????????????????????????????????? |
| C. punctatus (Yixian 2005115) | ????????????????????????????????? |
| C. punctatus (Yixian 2010158) | ????????????????????????????????? |
| C. zherikhini (Yixian 2006101) | ????????????????????????????????? |
| C. zherikhini (Yixian 2005113) | ????????????????????????????????? |
| C. zherikhini (Yixian 2005114) | ????????????????????????????????? |
| C. zherikhini (Yixian 2005109) | ????????????????????????????????? |
| C. zherikhini (Yixian 2005112) | ????????????????????????????????? |
| C. zherikhini (Yixian 2005103) | ????????????????????????????????? |
| Cretonanophyes asiaticus (sp1) | ??????????????????????????????110 |

| | |
|---|---|
| Cretonanophyes neocomicus (sp2) | ??????????????????????????????110 |
| Jarzembowskia edmundi | 10????????????????????????????110 |
| Baissacarodes sibiricus | ??????????????????????????????110 |
| Emanrhynchus lebedevi | ??????????????????????????????110 |
| Gobicar ponomarenkoi | ??????????????????????????????110 |
| Gobicar ulugeiensis | ??????????????????????????????110 |
| Mesophyletis calhouni | ??????????????????????????????110 |
| Hispanocar kseniae | ??????????????????????????????110 |
| Martinsnetoa dubia | ????????????????????????????????? |
| Cretocar luzzii | ??????????????????????????????110 |
| Montsecanomalus zherikhini | ????????????????????????????????? |
| Zigras cornus | ??????????????????????????????110 |
| Zigras nudicornus | ??????????????????????????????110 |
| Scabridus implexus | ?????????????????????100211???110 |
| Scabridus zigrasi | ??????????????????????????????110 |
| Anchineus dolichobothris | ??????????????????????????????110 |
| Caridae 1 | ??????????????????????????????110 |
| Caridae 2 | ??????????????????????????????110 |
| Caridae 3 | ??????????????????????????????110 |
| Preclarusbelus vanini | ????????????????????????????????? |
| Arariperhinus monnei | ????????????????????????????????? |
| Gratshevbelus erici | ????????????????????????????????? |
| Proterhinus sp. | --1002101111121111010101000200110 |
| Rhopalotria bicolor | 111003101011121011010101000200110 |
| Parallocorynus bicolor | 101003101011121011010101000200110 |
| Baltocar succinicus | ??????????????????????????????110 |
| Haplorhynchites aeneus | 101002000101101011210100111200110 |
| Involvulus hirtus | 101002010101101011210100111200110 |
| Merhynchites bicolor | ??1002011101101001210100211200110 |
| Eugnamptus punctatus | 101002010101101001010100211000110 |
| Auletobius cassandrae | 101002010111101001010110210000110 |
| Minurus testaceus | ??1002011011101001010100210000110 |
| Pseudauletes sp. | 101002010101101100210100210200110 |
| Byctiscus populi | ??1002011101101001010100210000110 |
| Listrobytiscus corvinus coeruleipennis | ??1002011101101001210100210100110 |
| Deporaus glastinus | 101002010011101011010110211200110 |
| Pterocolus ovatus | 101002010011101011010100210200110 |
| Homeolabus analis | 101002011101102011210102221000110 |
| Attelabus nigripes | 101002010101102001210102221020110 |
| Omolabus conicollis | ??1002011101101001010100211000110 |
| Euscelus dentipes | 101002010101102001010102221100110 |
| Henicolabus octospilotus | 101002010101102001010102221220110 |
| Lamprolabus sandacanus | ??1002011101101001010100211000110 |
| Euops quadrifasciculatus | 101002000101102001010102221220110 |
| Pilolabus viridans | 101002010001102011010100221020110 |
| Apoderus sp. | 101002010101101001010100221010110 |
| Parapoderus flavoebenus | ??1002010101101001010100221010110 |
| Clitostylus badeni | ??1002010101101001010102221020110 |
| Holapoderus hystrix | 101002010101101001010102221010110 |
| Paroplapoderus pardalis | ??1002010101101001010102221020110 |
| Cynotrachelus roelofsi | 101002010101101001010102221010110 |
| Trachelophorus giraffa | ??1002010101101001010102221020110 |
| Ithycerus novemboracensis | 101003001011102001000100211200110 |
| Brentus anchorago | 111023000012101101010101101001110 |
| Arrhenodes minutus | 111023000012101101010101101001110 |
| Henarrhenodes macgregori | ??1023010012101101010101001001110 |
| Baryrrhynchus schroderi | ??1023010012101101010101001001110 |
| Amorphocephala imitator | 111023000012101101010101001001110 |
| Antliarhinites zamiae | 011024000012101101010101100000110 |
| Cylas formicarius elegantulus | 111003000011102101010100001000110 |
| Oncodemerus sennai | ??1003101002102101010100001000110 |
| Stereodermus latirostris | 011003000011102101010100111001110 |

| | |
|---|---|
| Cerobates sexsulcatus | ??1003101002102101010100001000110 |
| Taphroderopsis oscillator | ??1003111002102101010100001000110 |
| Paratrachelizus uncimanus | 011023000012101101010100111001110 |
| Miolispa robusta | ??1003110002102101010100001001110 |
| Nemocephalus guatemalensis | 111003001011101101010100011001110 |
| Diuris shelfordi | ??1003101011102101010100001001110 |
| Ithystenus hollandiae | ??1023000002102101010100001001110 |
| Schizotrachelus bakeri | ??1003110002102101010100001001110 |
| Hormocerus scrobicollis | ??1023110002101101010100001001110 |
| Ulocerus sp. | 111003001012101100020100111001110 |
| Aporhina sp. | 120003001012101100010101011000310 |
| Apion longirostre | 111025001011122100010100201000110 |
| Sayapion arizona | ??1005001211102100010100211000110 |
| Perapion punctinasum | 111005001011102101010100201000110 |
| Phrissotrichum tubiferum | ??1025001211102100010100211000110 |
| Alocentron attenuatum | 111025001011122100010100201000110 |
| Aspidapion radiolus | ??1025001011102100010100211000110 |
| Ceratapion basicorne | 111025001011122100010100101000110 |
| Omphalapion hookeri | ??1025001011102100010100211000110 |
| Cybebus dimidiatus | 111005001011121100010100101000110 |
| Exapion ulicis | ??1025001011102100010100211000110 |
| Ixapion herculanum | ??1025002011122100010100211000110 |
| Kalcapion flavofemoratum | 111005002011002100010101101000110 |
| Melanapion minimum | ??1025002011122100010100211000110 |
| Malvapion malvae | 111025001011121100010100101000110 |
| Rhopalapion longirostre | ??1025002011122100010100211000110 |
| Noterapion meorrhynchum | ??1025011012001100010100211000110 |
| Eutrichapion alakanum | 111025001011122100010100211000110 |
| Capapion seniculus | ??1025002011120100010100211000110 |
| Stenopterapion tenue | ??1005001011122100010100211000110 |
| Trichapion gracilirostre | 111025001011122100010100211000110 |
| Chrysapion auctum | 111005001011122100010100211000110 |
| Protapion apricans | ??1025001011122100010100211000110 |
| Tanaos bicolor | 111004001011102101010100211000110 |
| Nanophyes canadensis | 111004001011101101010101101000100 |
| Dieckmanniellus nitidulus | 111004001011101101010101101000100 |
| Corimalia tamarisei | 111004001011001101010101101000100 |
| Allomalia quadrivirgata | 111004001011001101010101101000100 |
| Bracycerus sp. | --1003000111102101010201001100110 |
| Microcerus costalis | --1003000011102111010201001100110 |
| Episus gibbosus | ??1003101112102011010201001000110 |
| Ocladius obliquesetosus | --1003010011002111010101111000110 |
| Desmidophorus sp. | 021003011011002001010101211100112 |
| Dryophthorus americanus | --1010002111102001010101211100110 |
| Stenommatus sulcifrons | ??1010002111102001010101211030110 |
| Cryptoderma sp. | 121001001101002001010101211030301 |
| Orthognathus subparallelus | 121001001101102011010101211130111 |
| Mesocordylus bracteolatus | ??1011011101102011010100211030110 |
| Yuccaborus frontalis | 021001014111102011010101211130311 |
| Rhinostomus thompsoni | ??1001011101102011010101111030110 |
| Rhynchophorus palmarum | ??1001101101122011210101111130110 |
| Otidognathus sp | ??1001001101122011210101111130111 |
| Diocalandra frumenti | 021011004111022011010101211100110 |
| Toxorhinus baonii | 011011004101022011010101211100110 |
| Sitophilus oryzae | ??0001014101022000010101111130110 |
| Aphiocephalus guerini | 011001004111122011010101211130110 |
| Ommatolampus paratasioides | ??1001004101122011010101111130110 |
| Polytus mellerborgii | 011011004111002011010101211000310 |
| Rhodobaenus tredecimpunctatus | 011011004111122001010101211130310 |
| Scyphophorus acupunctatus | ??0001014101022011010101211200110 |
| Strombocerinae gen. sp. | --1011001111122011010101211200110 |
| Notaris (Erirrhinus) festuca | 111003001111122001010101211130110 |

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|---|---|
| Grypus leechi | 111003001111122001010101211130110 |
| Lissorhoptrus simplex | 111003002111122001010110211000110 |
| Stenopelmus rufinasus | 111001004001122001010101111100110 |
| Tanysphyrus lemnae | 111013004001122001000101111100110 |
| Tadius erirhinoides | 111003011001122101000100001100110 |
| Philacta testacea | ??1003104003022001010100001100110 |
| Alaocybites sp. | --1002002011022001011100211100110 |
| Gilbertiola sp. | --1002002011022001011100211100110 |
| Schizomicrus caecus | --1002004011022001001100211100110 |
| Perieges bardus | --1003001111121001001100211100110 |
| Antiquis opaque (French amber) | ???????????????????????????????11 |
| Curculio pardalis | 011010102001022000010100211100111 |
| Shigizo sp | ??1000102001122000010101001100112 |
| Carponius axillaris | ??1000102001022000010101001100112 |
| Timola sp | ??1000102001122000010100211100111 |
| Acalyptus carpini | ??1000102101122001010100211100110 |
| Amorphoidea lata | ??1000102101122001010100211100112 |
| Acentrus histrio | ??1000102101122001010100211100110 |
| Anoplus plantaris | ??1001102101122001010100211100110 |
| Cionopsis lineola | ??1001002101022001010100211100100 |
| Anthonomus fulvus | ??1001102101022001010100211100101 |
| Camarotus sp | ??1001102001122001010100211100111 |
| Odontopus calceatus | ??1001102001122001010100211100111 |
| Ceratopus sp. | ??1010112111022000010100211110111 |
| Cionus hortulanus | ??10101020011220000101002111?0110 |
| Stereonychus fraxini | ??1010102101022000010100211100110 |
| Haplonyx scutellatus | ??1001102101022001010100211100102 |
| Derelomus basalis | ??1010002101022001000100211100112 |
| Phyllotrox (Euclyptus) sp. | ??1010102101122001000100211000110 |
| Ellescus ephippiatus | ??1001102111122001010100211000110 |
| Dorytomus mucidus | 011001102111122001010100211100110 |
| Sicoderus tinamus | ??1001102001122001010100211000310 |
| Ludovix fasciatus | ??1001102001122001010100211100310 |
| Rhopalomerus tenuirostris | ??1001102101122001010100211000110 |
| Meriphus sp | ??1001102101122001010100211000110 |
| Geochus tibialis | ??1001002101022001010100211000110 |
| Gymnaetron tetrum | ??1001102112122000010100211100110 |
| Myrmex chevrolati | 021001102110122001010100211100310 |
| Piazorhinus sp. | ??1001102111022001010100211100110 |
| Pyropus cyaneus | ??1010002101122000010100211100102 |
| Isochnus rufipes | ??1001102111122000010100211100110 |
| Tachygonus centralis | 111001102111122000010100211100110 |
| Promecotarsus sp. | ??1001102111122000010100211130110 |
| Terires sp. | ??1001102111122000010100211100110 |
| Styphlus penicillus | ??1001102111122000010100211100110 |
| Tychius picirostris | ??1010102011022001010100211100111 |
| Lignyodes horridulus | 111010102001022001010100211100111 |
| Ulomascus parallelus | ??1000112011122000010100210000111 |
| Bagous transversus | 111001102110122001010100211100110 |
| Pnigodes setosus | 111001102110122001010100211100110 |
| Hydronomus sinuatocollis | 111001004110122001010100211100110 |
| Baris torquata | 111001102110122000010100211100301 |
| Anthinobaris dispilota | ??1001102100122000010100211100301 |
| Limnobaris bicincta | ??1001103100122000010100211100301 |
| Torcus nigrinus | ??1001102100122001011100211100301 |
| Nicentrus grossulus | ??1001102100122001011100211100301 |
| Calandrinus grandicollis | ??1001003100122001011100211100301 |
| Eisonyx crassipes | ??1001113113122000010100211100102 |
| Pycnobaris pruinosa | 111001102110122000010100211100302 |
| Thanius sp. | 111001102110122000010100211100302 |
| Xystus ater | ??1001102101122001010100211100301 |
| Madopterus talpa | ??1001103103022001010100211100302 |

| | |
|---|---|
| Peridinetus irroratus | ??1001102103122001010100211100301 |
| Barinus bivittatus | ??10011031001220010101002111003 01 |
| Sibariops concurrens | ??10011021001220010101002110003 01 |
| Diorymeropsis xanthoxyli | ??10011021001220010101002111003 01 |
| Mononychus punctumalbum | 11101010211102200101010321110030 2 |
| Pelenomus roelofsi | ??10001021111220010101032111003 02 |
| Rhinoncus perpendicularis | ??10001021111220010101032111003 12 |
| Scleropterus serratus | ??10001021110220010101032111003 10 |
| Rutidosoma globulus | ??10001021111220010101032111003 11 |
| Homorosoma asperum | ??10001021111220010101032111003 12 |
| Amalus scortillum | ??10001021111220010101032111003 11 |
| Ceutorhynchus nitidulus | 11100010211312200101010321120031 2 |
| Cardipennis sulcithorax | ??10001021110220010101032110003 12 |
| Dieckmannius sexnotatus | ??10001021110220010101032110003 12 |
| Coeliodes rana | ??10001021110220010101032111003 11 |
| Mecysmoderes euglyptus | ??10001021110220000101002111003 01 |
| Xenysmoderodes sasajii | ??10001021110220000101002111003 01 |
| Augustinus comes | 11100010221312200001010021110031 2 |
| Auleutes epilobii | ??10001032110220000101002111003 02 |
| Cyphosenus citricola | ??10001022110220010101002111003 02 |
| Anthypurinus haloxylicola | ??10001022110220010101032111003 02 |
| Lioxyonyx fausti | ??10001022111220010101032110003 02 |
| Arachnobas gazella | ??10011021111220010101002111001 12 |
| Campyloscelus westermanni | ??10011021111220010101032111001 02 |
| Metialma straminea | 11101010211312200101010021110010 2 |
| Cyllophorus fausciatus | ??10010021111220010101002111001 02 |
| Acoptus suturalis | ??10010020011220010101002111001 10 |
| Lobotrachelus troglodytes | ??10010021111220010101032111001 01 |
| Mecopus trilineatus | 11100110211012200101010021110011 1 |
| Telephae oculata | ??10101020110220010101032111003 01 |
| Balanogastris kolae | ??10001020011220010101032110003 01 |
| Cratosomus "punctulatus" | ??10011021111220010101032111003 11 |
| Trichodocerus sp. | ??10012021110220010101032111001 11 |
| Cylindrocopturus operculatus | ??10011021111220010101032111003 10 |
| Cylindrocopturus adspersus | 11100110211112200101010321110031 0 |
| Hoplocopturus sp. | ??10111021211220010101032111003 10 |
| Cossonus impressifrons | 11001010211112200101010021110011 0 |
| Acamptus echinus | ??00101021111220010101002111301 10 |
| Araucarius sp. | 11001010211112200101010021110011 0 |
| Catolethrus sp. | ??00101021111220010101002111001 10 |
| Pseudopentarthrum atrolucens | ??00101021111220010101002111001 10 |
| Macroscytalus chisosensis | ??00001021111220010101002111001 10 |
| Proeces depressus | ??00001021111220010101002111001 10 |
| Pseudapotrepus sp. | ??10001021111220010101002111001 11 |
| Elassoptes marinus | ??00001021111220010101002110001 11 |
| Heptarthrum sp. | -11000102111122001010100211100110 |
| Phloeophagus minor | ??00001021111220010101002111001 10 |
| Cryptorhynchus lapathi | 12101010210112200101010021110111 1 |
| Coelosternus sp. | ??10011031111220010101002111011 12 |
| Eurhoptus sp. | ??10101031110220010101002111001 12 |
| Gerstaeckeria lecontei | ??10011021111220010101002111001 12 |
| Aedemonus erichsoni | ??10011021111220010101002111001 01 |
| Mechistocerus sp. | 12100110211112200101010021120010 1 |
| Camptorhinus sp. | ??10101020111220010101002112001 12 |
| Cophes obtenus | ??10111021111220010101002111011 12 |
| Psepholax humilis | ??10101021111220010101002111011 12 |
| Strongylopterus ovatus | --10101021111220010101002112011 12 |
| Torneuma subpanum | ??10001021111220010101002112011 11 |
| Bronchus (Hipporhinus) bohemani | --10000032011220011102002111001 10 |
| Amycterus elongata | ??10200022011220011102002111001 10 |
| Aegorhinus nodipennis | 11100010211112200101010021100011 0 |
| Diabathrarius sp. | ??10001021111220010101002110001 10 |

| | |
|---|---|
| Gonipterus gibberus | ??1000102111122001010100211100110 |
| Emphyastes fucicola | --1001102111122001010100211100110 |
| Listroderes costirostris | ??1020102101122001010100211100111 |
| Agraphus bellicus | ??1000003100122001010103110100110 |
| Lepidophorus lineaticolllis | --1000102100122101010100211100110 |
| Anypotactus jansoni | ??1000102100122001010103000000110 |
| Strophosoma melanogrammus | ??1001002110122001010103100000110 |
| Brachyderes lusitanicus | ??1001002110122001010103100000111 |
| Trigonops platessa | ??1000002104022001010103200000111 |
| Cneorrhinus geminatus | ??2100002100122001010103231000110 |
| Cratopus viridisparsus | ??2101003100022001010103231000111 |
| Cyrtepistomus castanaeus | ??2001002100122001010103200000110 |
| Palirhoeus eatoni | ??2101002114122001010103231000110 |
| Elytrurus griseus | ??2101003101122001010103231000110 |
| Episomus lentus | ??2101003104122001010103231000110 |
| Eudiagogus pulcher | ??2000003100122001000103200100111 |
| Colecerus (Coleocerus) marmoratus | ??2000002100122001000103000100111 |
| Eucoleocerus (Eucolecerus) sp. | ??2000002100122001000103000100311 |
| Eupholus bennetti | ??2001002104122101010103200100310 |
| Compsus argyreus | 122001002104122101000103000100310 |
| Lachnopus floridanus | --2001003104122001010103000200310 |
| Hormorus undulatus | ??2001102104122001010103200000310 |
| Leparocerus morio | ??2001002104122001010203000000110 |
| Hypoptus macularis | ??2101002104122001010103230000310 |
| Cyrtomon (Cyphus) lautus | ??2001002104022001010103100000310 |
| Naupactus (Graphognathus) peregrinus | ??2001003104122001010100200000110 |
| Ophryastes (Eupagoderes) argentatus | ??2101003104122001010200230000110 |
| Sciopithes obscurus | ??2101002104122001010103230000110 |
| Pachyrrhynchus tobafolius | ??2000103110122001010103100000110 |
| Stomodes gyrosicollis | ??2101003104122001010103230200110 |
| Rhinospathe albomarginata | ??2101003104122001010103230200311 |
| Liophloeus nubilis | ??2101003104122001010103230000110 |
| Premnotrypes vorax | ??2101002104122001010103230000310 |
| Prypnus scutellaris | ??2101003100022001010103200000310 |
| Rhyncogonus gracilis | ??2101003104122001010103230000110 |
| Mitostylus tenius | ??2000102004022001010100100000110 |
| Sitona californicus | 122001102104122001010110211200310 |
| Pachnaeus litus | ??2101003104122001010103230200301 |
| Tanyrhynchus sp. | ??2001002110122001000103000000110 |
| Trachyphloeus aristatus | ??2101002104122001010103230000110 |
| Rhigopsis effracta | ??2101002104122001010103200000310 |
| Dasydema hirtella | ??2101002104122001010103200000110 |
| Hypera punctata | 121010102104122101010110211320111 |
| Coniatus tamaricis | 121010102104022101010110211300111 |
| Tylopterus pallidus | 121010102104122101010110211100111 |
| Cepurellus cervinus | ??1010102104122101010110211100112 |
| Lixus concavus | 121010103111122001010100211100302 |
| Larinus carlinae | 121000102111122001010100211100302 |
| Apleurus (Dinocleus) molitor | 121000102111122001010100211100302 |
| Stephanocleonus sp. | ?21000102111122001010100211100302 |
| Rhinocyllus conicus | 121000102111122001010100211100302 |
| Bangasternus orientalis | ?21000102111122001010100211100302 |
| Laemosaccus nephele | 111001102110122101010103211110311 |
| Neolaemosaccus (Saccolaemus) carinicollis | 111001102110122101010103211130311 |
| Magdallis armicollis | 111001102110122101010103211100311 |
| Liparus glabrirostris | ??1001102101122101010100211100110 |
| Acicnemis sp. | ??1010103113122101010100211100111 |
| Amorphocerus sp. | ??1010103113122101010100211100311 |
| Rhyparonotus sp. | ??1000103103122101010100211200311 |
| Cholus rana | ??1001102111122101010100211100312 |
| Rhyssomatus lineaticollis | 121001102111122101010103211100112 |
| Cleogonus sp. | ??1000102111122101010103211100302 |

| | |
|---|---|
| Conotrachelus fissunguis | 121001102110122101010103211100101 |
| Gononotus angulicollis | ??1000102111122101010100211100111 |
| Guioperus trifasciatus | ??1001102111122101010100211100112 |
| Heilus bioculatus | ??1001102111122101010100211100311 |
| Heilipodus polygluttatus | ??1001102111122101010100211100301 |
| Hylobius pales | ??1001102111122101010100211100311 |
| Ithyporus stolidus | 121010102001122101010100211110311 |
| Sclerocardius africanus | ??1010102001122101010100211110311 |
| Lepyrus palustris | ??1010102001122101010100211130312 |
| Lymantes sandersoni | ??1001102111022101010103211100311 |
| Alcidodes dentipes | ??1001102111022101010100211100302 |
| Nettarhinus bilobus | ??1001102111022101010100211200311 |
| Petalochilus gemellus | ??1001103111122101010103211100302 |
| Phrynixus sp. | ??1001102111122101010100211131312 |
| Pissodes strobi | ??1001102111122101010100211100312 |
| Sternechus paludatus | ??2001102111122101010100211101112 |
| Neophycoroetes testaceus | ??1001102111122101010100211100110 |
| Trigonocolus curvipes | ??1001102110122101010100211100302 |
| Trypetes sp. | ??1001102111122101010100211100311 |
| Parorobitus gibbus | ??1001122121122101010100211100102 |
| Scolytogenes expers | 110110202211122111010112221320110 |
| Scolytoplatypus tycon | 010110202211122101010112221320211 |
| Xyleborus spathipennis | 010110202211122111010112221320311 |
| Sphaerotrypes pila | 012110202211122111010112221320101 |
| Alniphagus costatus | 010110202111122101010112221320110 |
| Pityophthorus jucundus | 010110202111122111010112221320111 |
| Hylurgops planirostris | 010110202111122111010112221320111 |
| Tesserocerus inermis | 010110002001120111022112221020310 |
| Scolytus multistriatus | 110110002111120011010112221000111 |
| Platypus parallelus | 110110002001120101022112221020110 |
| Ficicis despectus | 010110002111122101010112221320110 |
| Dendroctonus micans | 010110002111122101010112221320110 |
| Diapus aculeatus | 110110002001120111022112221020110 |
| Cylindrobrotus pectinatus (Lebanese amber) | ??????????????????????????????110 |
| Microborus inertus (Burmese amber) | ??????????????????????????????110 |
| indet 4 nemonychid (Yixian 2007104 1/2) | ??????????????????????????????11? |
| indet 3 nemonychid (Yixian 2010159) | ??????????????????????????????11? |
| indet 2 nemonychid (Yixian 2005111) | ??????????????????????????????11? |
| Microprobelus liuae (Yixian 2005106) | ??????????????????????????????11? |
| Microprobelus liuae (Yixian 2007102) | ??????????????????????????????11? |
| Chinocimberis augustipecteris (Yixian 2007104) | ??????????????????????????????11? |
| Chinocimberis augustipecteris (Yixian 2005127) | ??????????????????????????????11? |
| Chinocimberis magnoculi (Yixian 2010155) | ??????????????????????????????11? |
| Chinocimberis magnoculi (Yixian 2005107) | ??????????????????????????????11? |
| Chinocimberis augustipecteris (Yixian 2005102) | ??????????????????????????????11? |
| Renicimberis latipecteris (Yixian 2005123) | ??????????????????????????????11? |
| Renicimberis latipecteris (Yixian 2010153) | ??????????????????????????????11? |
| Renicimberis latipecteris (Yixian 2005101) | ??????????????????????????????11? |
| Renicimberis latipecteris (Yixian 2007101) | ??????????????????????????????11? |
| A. concavus (Yixian 2007105) | ??????????????????????????????11? |
| A. brachyorhinos (Yixian 2005105) | ??????????????????????????????110 |
| A. brachyorhinos (Yixian 2005119) | ??????????????????????????????11? |
| A. brachyorhinos (Yixian 2005125) | ??????????????????????????????11? |
| A. macilentus (Yixian 2007103) | ??????????????????????????????11? |
| A. macilentus (Yixian 2010151) | ??????????????????????????????11? |
| A. macilentus (Yixian 2010157) | ??????????????????????????????11? |
| A. macilentus (Yixian 2006102) | ??????????????????????????????11? |
| A. macilentus (Yixian 2005110 1/2) | ??????????????????????????????110 |
| Abrocarina undet. 1 (Yixian 2010154) | ??????????????????????????????11? |
| A. relicinus (Yixian 2010152) | ??????????????????????????????11? |
| A. relicinus (Yixian 2005116 1/2) | ??????????????????????????????11? |
| A. relicinus (Yixian 2005118) | ??????????????????????????????11? |

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|---|---|
| A. relicinus (Yixian 2005117) | ??????????????????????????????11? |
| A. relicinus (Yixian 2005122) | ??????????????????????????????11? |
| A. relicinus (Yixian 2010160) | ??????????????????????????????11? |
| A. macilentus (Yixian 2010156) | ??????????????????????????????11? |
| Archaeorrhynchus acutirostris | ????????0?????????????????0???11? |
| Archaeorrhynchus latitarsus | ????????0?????????????????0???11? |
| Archaeorrhynchus paradoxopus | ????????0?????????????????0???11? |
| Archaeorrhynchus kryzhanovskyi | ????????0?????????????????0???11? |
| Archaeorrhynchus nikolaevi | ????????0?????????????????0???11? |
| Archaeorrhynchus carpenteri | ????????0?????????????????0???11? |
| Archaeorrhynchus sukatshevai | ????????0?????????????????0???11? |
| Archaeorrhynchoides crowsoni | ????????0?????????????????0???11? |
| Archaeorrhynchoides arnoldii | ????????0?????????????????0???11? |
| Kararhynchus occiduus | ????????0?????????????????0???11? |
| Eobelus longipes | ????????0?????????????????0???11? |
| Eobelus sp. | ????????0?????????????????0???11? |
| Belonotaris karatavicus | ????????0?????????????????0???11? |
| Probelus tibialis | ????????0?????????????????0???11? |
| Probelus cockerelli | ????????0?????????????????0???11? |
| Probelus scudderi | ????????0?????????????????0???11? |
| Probelus longitarsus | ????????0?????????????????0???11? |
| Probelus curvispinus | ????????0?????????????????0???11? |
| Probelus handlirschi | ????????0?????????????????0???11? |
| Probelopsis acutiapex | ????????0?????????????????0???11? |
| Arnoldibelus wanatavieus | ????????0?????????????????0???11? |
| Arnoldibelus gratshevi | ????????0?????????????????0???11? |
| Arnoldibelus zherichini | ????????0?????????????????0???11? |
| Arnoldibelus medvedevi | ????????0?????????????????0???11? |
| Arnoldibelus rasnitsyni | ????????0?????????????????0???11? |
| Arnoldibelus rohdendorfi | ????????0?????????????????0???11? |
| Arnoldibelus wickhami | ????????0?????????????????0???11? |
| Arnoldibelus korotyaevi | ????????0?????????????????0???11? |
| Arnoldibelus heeri | ????????0?????????????????0???11? |
| Arnoldibelus martynovi | ????????0?????????????????0???11? |
| Arnoldibelus karatavicus | ????????0?????????????????0???11? |
| Nanophydes ovatus | ????????0?????????????????????11? |
| Ampliceps dentitibia | ????????0?????????????????????11? |
| Ampliceps furcitibia | ????????0?????????????????????11? |
| Oxycorynoides progressivus | ????????0?????????????????????11? |
| Karataucarodes zimmermanni | ????????0?????????????????????11? |
| Scelocamptus dubius | ????????0?????????????????????11? |
| Scelocamptus curvipes | ????????0?????????????????????11? |
| Oxycorynoides rohdendorfi | ????????0?????????????????????11? |
| Oxycorynoides brevipes | ????????0?????????????????????11? |
| Oxycorynoides zherichini | ????????0?????????????????????11? |
| Oxycorynoides similis | ????????0?????????????????????11? |
| Belonartis lineatipunctatus | ????????0?????????????????????11? |
| Oxycorynoides mongolicus | ????????0?????????????????????11? |
| Oxycorynoides gurvanensis | ????????0?????????????????????11? |
| Eccoptarthroides longirostris | ????????0?????????????????????11? |
| Eccoptarthroides ponomarenkoi | ????????0?????????????????????11? |
| Eccoptarthroides martynovi | ????????0?????????????????????11? |
| Eccoptarthroides nikitskyi | ????????0?????????????????????11? |
| Pseudobrenthorrhinus magnus | ????????0?????????????????????11? |
| Pseudobrenthorrhinus crassicornis | ????????0?????????????????????11? |
| Brenthorrhinus mirabilis | ??????????????????????????????11? |
| Gobibrenthorrhinus gigas | ??????????????????????????????11? |
| Brenthorrhinus brevirostris | ??????????????????????????????11? |
| Brenthorrhinoides mandibulatus | ??????????????????????????????11? |
| Scelocamptus tenuirostris | ??????????????????????????????11? |
| Brenthorrhinoides robustus | ??????????????????????????????11? |
| Brenthorrhinoides pubescens | ??????????????????????????????11? |

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|---|---|
| Mongolbrenthorrhinus arnoldii | ??????????????????????????????11? |
| Mongolbrenthorrhinus pusillus | ??????????????????????????????11? |
| Mongolbrenthorrhinus flavus | ??????????????????????????????11? |
| Testudobrenthorrhinus baissiensis | ??????????????????????????????11? |
| Testudobrenthorrhinus taetricus | ??????????????????????????????11? |
| Buryatnemonyx niger | ??????????????????????????????11? |
| Buryatnemonyx tener | ??????????????????????????????11? |
| Buryatnemonyx gratshevi | ??????????????????????????????11? |
| Oxycorynoides ponomarenkoi | ??????????????????????????????11? |
| Procurculio fortipes | ??????????????????????????????11? |
| Procurculio pallens | ??????????????????????????????11? |
| Megabrenthorrhinus grandis | ??????????????????????????????11? |
| Megabrenthorrhinus longicornis | ??????????????????????????????11? |
| Eccoptarthrus crassipes | ??????????????????????????????11? |
| Eccoptothorax latipennis | ??????????????????????????????11? |
| Distenorrhinus pallidirostris | ??????????????????????????????11? |
| Distenorrhinus ovatus | ??????????????????????????????11? |
| Distenorrhinus arnoldii | ??????????????????????????????11? |
| Distenorrhinus elongatus | ??????????????????????????????11? |
| Distenorrhinus rotundicollis | ??????????????????????????????11? |
| Distenorrhinus angulatus | ??????????????????????????????11? |
| Distenorrhinus major | ??????????????????????????????11? |
| Distenorrhinus antennatus | ??????????????????????????????11? |
| Paroxycorynoides elegans | ??????????????????????????????11? |
| Selengarhynchoides sharyngolensis | ??????????????????????????????11? |
| Selengarhynchus ovalis | ??????????????????????????????11? |
| Pseudonemonyx stupendus | ??????????????????????????????11? |
| Cretonemonyx minimus | ??????????????????????????????11? |
| Cretonemonyx longirostris | ??????????????????????????????11? |
| Cretonemonyx profligatus | ??????????????????????????????11? |
| Megametrioxenoides longus | ??????????????????????????????11? |
| Megametrioxenoides proelomus | ??????????????????????????????11? |
| Cretoxenoides erdeniensis | ??????????????????????????????11? |
| Chinocimberis dispersus | ??????????????????????????????11? |
| Baissimberis prodigiosus | ??????????????????????????????11? |
| Mongolocar orcinus (nemonychid) | ??????????????????????????????11? |
| Karacar contractus (nemonychid) | ??????????????????????????????11? |
| Baissabrenthorrhinus mirabilis | ??????????????????????????????11? |
| Ulyaniana nobilis | ??????????????????????????????11? |
| Ulyaniana excellens | ??????????????????????????????11? |
| Ulyanisca dentipes | ??????????????????????????????11? |
| Slonik sibiricus | ??????????????????????????????11? |
| Hyperites nadezhkini | ??????????????????????????????11? |

TABLE 8. Characters 231 - 263

| | 231  236  241  246  251  256  261 |
|---|---|
| | \|    \|    \|    \|    \|    \|    \| |
| Cucujus clavipes | 000011000000010010001000120010000 |
| Orsodacne atra childreni (Orsodacnidae) | 000001001000010000001000120000100 |
| Fidia viticida (Chrysomelidae) | 010011000000000010001000120000001 |
| Cimberis sp. | 100011001000010000001000120100000 |
| Nannomacer germaini | 100011001000010000001000020000000 |
| Mecomacer scambus | 100011001000010000001000020000000 |
| Rhynchitomacerinus kuscheli | 100011001000010000001000120000000 |
| Nemonyx lepturoides | 100001001000010010001000120010000 |
| Doydirhynchus austriacus | 100011001000010000001000120010000 |
| Lecontellus byturoides | 100011001000010000001000120010000 |
| Arra similis (Spanish amber) | 100011??10000?0?0???????????????? |
| indet 5 anthribid (Yixian 2005126) | ????????????????????????????????? |
| Trigonorhinus sp. | 100011101000210000201000020000000 |
| Anthribus nebulosus | 100011101000210000201000020000000 |

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|---|---|
| Epicerastes sp. | 100011111000210000001000020110000 |
| Apolecta samarana | 100011111000010000001000020110000 |
| Gynandrocerus sp. | 100011110000110000001000020000000 |
| Phaenithon semigriseum | 102010111000120002002101020000000 |
| Basitropis sp. | 100011111000010000001000020000000 |
| Strabus bimaculatus | 102011111000010000001000020000000 |
| Corrhecerus sp | 102011111000010000002000020000000 |
| Straboscopus tessellatus | 102010100000210000200000020000000 |
| Euparius marmoreus | 102011100000100000001000020000000 |
| Discotenes nigrotuberculata | 102011100000100000001000020000000 |
| Ischnocerus infuscatus | 100011111000010000000000020110000 |
| Dendropemon sp. | 100011111000010000000000020000000 |
| Eucorynus crassicornis | 100011111000010000000000020000000 |
| Gymnognathus sp. | 102010110000110002002101020000000 |
| Dinema filicornis | 100011111000010000000000020000000 |
| Neseonos brunneus | 100011111000010000000000020000000 |
| Mauia subnotata | 100011111000010000000000020000000 |
| Illis anna | 102011111000010000001000020000000 |
| Mecocerus sp. | 100011111000210002200000020110000 |
| Acanthothorax basalis | 100011111000210002201000020110000 |
| Phloeophilus sulcifrons | 102011111000210002201000020000000 |
| Mycetis marginicollis | 102011111000210000201000020100000 |
| Ormiscus sp. | 102011101000010000002000020000000 |
| Ozotomerus bipunctatus | 102011111000110000001000020000000 |
| Piesocorynus sellatus | 102011111000010000001000020000000 |
| Brachycorynus distentus | 101011111000010000001000020000000 |
| Goniocloeus sp. | 102011111000010000001000020000000 |
| Platyrhinus resinosus | 102011111000110000201000020000000 |
| Phoenicobiella chamaeropis | 102011101000110000001000020000000 |
| Toxonotus fascicularis | 100011111000110000001000020000000 |
| Phloeobius pallipes | 102011111000110000000000020000000 |
| Platystomos wallacei | 102011111000110000000000020000000 |
| Ptychoderes sp. | 102010111000110000001000020000000 |
| Phloeotragus polyopras | 102010111000110000000000020110000 |
| Cerambyrhynchus schoenherri | 102010111000110000000000020000000 |
| Rhinotropis superciliaris | 102010111000110000201000020000000 |
| Sintor quadrilineatus | 102011100000100000201000020000000 |
| Allandrus bifasciatus | 102010110000010000001000020000000 |
| Stenocerus sp. | 102010111000010000001000020000000 |
| Plintheria plintheroides | 102011111000010000201000020000000 |
| Trigonorhinus sticticus | 100011111000110002002101020000000 |
| Tropideres fasciatus | 102010111000210000202101020000000 |
| Acorynus pallipes | 102011111000210000201101020000000 |
| Cedus guttatus | 102011111000210000201101020000000 |
| Xenocerus ancyra | 102011101000210000200000020000000 |
| Xylinada rugicollis | 102011111000010000000000020000000 |
| Stiboderes westermanni | 102011111000010000000000020000000 |
| Exechesops bakeri | 102011101000010002201000020000000 |
| Holostilpna sp. | 102011100000210002201000020000000 |
| Choragus sayi | 102011100000010000201000020000000 |
| Euxenus jordani | 102011111000010000201000020000000 |
| Araecerus levipennis | 102011100000210002201000020000000 |
| Acaromimus americanus | 102011001000010000000000020000000 |
| Misthosima sp. | 100011111000210002201000020000000 |
| Cisanthribus sp. | 102011001000010000000000020000000 |
| Notioxenus ater | 102011111000010000001000020000000 |
| Urodon rufipes | 100011101000010001001100020000000 |
| Rhinotia sp. | 000000002001120002212101102100010 |
| Belus semipunctatus | 000000002001020002212100102110010 |
| Homalocerus lyciformis | 000010102001110000001000002110010 |
| Pachyura australis | 000010002001010100001101021010000 |
| Dicordylus marmoratus | 000010002000010100001000001010000 |

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|---|---|
| Daohugou belid sp. | 0000100?200?0???0????????????????? |
| Montsecbelus solutus | ???0?????????????????????????????? |
| Car sp. | 1010001112001101000000000120010010 |
| Car condensatus | 1010001112001101000000000120010010 |
| Caenominurus topali | 1000201110001101000010001200100101 |
| Albicar contriti (Spanish amber) | 10000?1?1000?????????????????????? |
| Chilecar pilgerodendri | 1000201110001101000010001200100101 |
| Carodes revelatus | 10?0??111200??0????????????????010 |
| Baissorhynchus tarsalis | 1??0??1112???????????????????????? |
| Paleocar princeps | ???0?????????????????????????????? |
| Baissacar passarius | ???0?????????????????????????????? |
| Cretonanophyes longirostris | 1??00?1112???????????????????????? |
| Cretonanophyes punctatus | ???00?11?2???????????????????????? |
| C. punctatus (Yixian 2007105 1/2) | ?????????????????????????????????? |
| C. punctatus (Yixian 2006103) | ?????????????????????????????????? |
| C. punctatus (Yixian 2005115) | ?????????????????????????????????? |
| C. punctatus (Yixian 2010158) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2006101) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2005113) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2005114) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2005109) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2005112) | ?????????????????????????????????? |
| C. zherikhini (Yixian 2005103) | ?????????????????????????????????? |
| Cretonanophyes asiaticus (sp1) | ???00?111????????????????????????? |
| Cretonanophyes neocomicus (sp2) | 1??00?111????????????????????????? |
| Jarzembowskia edmundi | 1??0??111????????????????????????? |
| Baissacarodes sibiricus | 1??0??111????????????????????????? |
| Emanrhynchus lebedevi | ???0??111????????????????????????? |
| Gobicar ponomarenkoi | 1??0??111????????????????????????? |
| Gobicar ulugeiensis | ???0??111????????????????????????? |
| Mesophyletis calhouni | 1??0??111200?????????????????????? |
| Hispanocar kseniae | ???0??111????????????????????????? |
| Martinsnetoa dubia | ???0??111????????????????????????? |
| Cretocar luzzii | 1000?0111200??0??????????????????? |
| Montsecanomalus zherikhini | ???0??111????????????????????????? |
| Zigras cornus | 100000111000??0??????????????????? |
| Zigras nudicornus | 100000111000??0??????????????????? |
| Scabridus implexus | 100000111000??0??????????????????? |
| Scabridus zigrasi | 100000111000??0??????????????????? |
| Anchineus dolichobothris | 1000??110200?????????????????????? |
| Caridae 1 | 1??0??1112?0?????????????????????? |
| Caridae 2 | 1??0??111200?????????????????????? |
| Caridae 3 | 1??00?111100?????????????????????? |
| Preclarusbelus vanini | ???0?????????????????????????????? |
| Arariperhinus monnei | ???0?????????????????????????????? |
| Gratshevbelus erici | ???0?????????????????????????????? |
| Proterhinus sp. | 1000210002101110000010111200100101 |
| Rhopalotria bicolor | 1010110010000000210020010200100101 |
| Parallocorynus bicolor | 1000110010000000210021011200100101 |
| Baltocar succinicus | 1?10??1110???????????????????????? |
| Haplorhynchites aeneus | 1100010010001101100011001200000101 |
| Involvulus hirtus | 1100010010000101101010001200000101 |
| Merhynchites bicolor | 1100010010000101111011001200000101 |
| Eugnamptus punctatus | 1100010010000101100011001200000101 |
| Auletobius cassandrae | 1100010010000101100010001200000101 |
| Minurus testaceus | 1100010010000101100010001200000101 |
| Pseudauletes sp. | 1100010010000101122011001200000101 |
| Byctiscus populi | 1100210010000101101111001200000101 |
| Listrobytiscus corvinus coeruleipennis | 1100110010000101100111001200000101 |
| Deporaus glastinus | 1100010010000101100111001200000101 |
| Pterocolus ovatus | 1110010010000111100111011200000101 |
| Homeolabus analis | 1100010010000101100111011200001101 |

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|---|---|
| Attelabus nigripes | 110001001000010111011111120000110 |
| Omolabus conicollis | 110001001000010111011101120000110 |
| Euscelus dentipes | 110001001000010110011101120000110 |
| Henicolabus octospilotus | 110001001000010110011101120000110 |
| Lamprolabus sandacanus | 110001001000010111011101120000110 |
| Euops quadrifasciculatus | 110001001000010110111101120000110 |
| Pilolabus viridans | 110011001000010110111101120000110 |
| Apoderus sp. | 110011001000010110111101120000110 |
| Parapoderus flavoebenus | 110011001000010110111101120000110 |
| Clitostylus badeni | 110001001000010110111101120000110 |
| Holapoderus hystrix | 110011001000010110111101120000110 |
| Paroplapoderus pardalis | 110011001000010110111101120000110 |
| Cynotrachelus roelofsi | 110011001000010110111101120000110 |
| Trachelophorus giraffa | 110011001000010110111101120000110 |
| Ithycerus novemboracensis | 100020100010111100000100121000101 |
| Brentus anchorago | 100020101111211100001110120000100 |
| Arrhenodes minutus | 100020101111211100001110120000100 |
| Henarrhenodes macgregori | 100021101110211101100010120000100 |
| Baryrrhynchus schroderi | 100021101110211100001010120000100 |
| Amorphocephala imitator | 100021101110211100011010120000100 |
| Antliarhinites zamiae | 100021101110111100011010120000100 |
| Cylas formicarius elegantulus | 100021111110210110000010120000100 |
| Oncodemerus sennai | 100021101111211100001010120000100 |
| Stereodermus latirostris | 100021101111211110001010120010100 |
| Cerobates sexsulcatus | 100021101111211100001010120000100 |
| Taphroderopsis oscillator | 100021101111211100001010120000100 |
| Paratrachelizus uncimanus | 100021101111211100001010120010100 |
| Miolispa robusta | 100021101111211100001010120010100 |
| Nemocephalus guatemalensis | 100021101111211100001010120010100 |
| Diuris shelfordi | 100021101111211100000010120000100 |
| Ithystenus hollandiae | 100021101111211100000010120000100 |
| Schizotrachelus bakeri | 100021101111211100001010120000100 |
| Hormocerus scrobicollis | 100021101111211100000010120000100 |
| Ulocerus sp. | 100021101111211100001010120000100 |
| Aporhina sp. | 100021111110111110011111120000101 |
| Apion longirostre | 100021111112111110000010120000110 |
| Sayapion arizona | 100021111112111100001000120000110 |
| Perapion punctinasum | 100021111112111110001010120000110 |
| Phrissotrichum tubiferum | 100021111112111110001010120000110 |
| Alocentron attenuatum | 100021111112111110001010120000110 |
| Aspidapion radiolus | 100021111112111100001010120000110 |
| Ceratapion basicorne | 100021111112111110001010120000110 |
| Omphalapion hookeri | 100021111112111100001010120000110 |
| Cybebus dimidiatus | 100020110110111110000010120000110 |
| Exapion ulicis | 100021111112111100001010120000110 |
| Ixapion herculanum | 100021111112111100001010120000110 |
| Kalcapion flavofemoratum | 100021111112111100001010120000110 |
| Melanapion minimum | 100021111112111100001010120000110 |
| Malvapion malvae | 100021111110111110001010120000110 |
| Rhopalapion longirostre | 100021111110111100001010120000110 |
| Noterapion meorrhynchum | 100021111112111100001010120000110 |
| Eutrichapion alakanum | 100021111112111110001010120000110 |
| Capapion seniculus | 100021111112111100001010120000110 |
| Stenopterapion tenue | 100021111112111100001010120000110 |
| Trichapion gracilirostre | 100021111112111110000010120000110 |
| Chrysapion auctum | 1000211111121111?0001010120000110 |
| Protapion apricans | 100021111112111100001010110010110 |
| Tanaos bicolor | 100021101110111100001010120000110 |
| Nanophyes canadensis | 100021111110111110000010120000110 |
| Dieckmanniellus nitidulus | 100021111110111110000010120000110 |
| Corimalia tamarisei | 100021111110111110000010120000110 |
| Allomalia quadrivirgata | 100021111110111110000010120000110 |

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|---|---|
| Bracycerus sp. | 1000211010100-10100-----120000100 |
| Microcerus costalis | 100021111110011000000010120010100 |
| Episus gibbosus | 100021111110011000000010120010100 |
| Ocladius obliquesetosus | 100021110110011100000010110110100 |
| Desmidophorus sp. | 110021111110011110000010110110100 |
| Dryophthorus americanus | 110021101110211100000010310110011 |
| Stenommatus sulcifrons | 110021101110211100000010310110011 |
| Cryptoderma sp. | 110021100110111100000010320000011 |
| Orthognathus subparallelus | 110021101110211120000010310110011 |
| Mesocordylus bracteolatus | 110021101110211110000010320010011 |
| Yuccaborus frontalis | 110021100110211110000010320000011 |
| Rhinostomus thompsoni | 110021101110221110000010320000011 |
| Rhynchophorus palmarum | 110021101110221110000010020000011 |
| Otidognathus sp | 110021101110221110000010020000011 |
| Diocalandra frumenti | 110021100110121110000110320100011 |
| Toxorhinus baonii | 120021100110121110000110320100011 |
| Sitophilus oryzae | 110021101110221110000110320000011 |
| Aphiocephalus guerini | 110021101110221110000110320000011 |
| Ommatolampus paratasioides | 110021101110221110000110320000011 |
| Polytus mellerborgii | 110021100110121110000110320000011 |
| Rhodobaenus tredecimpunctatus | 120021100110221120000110320000011 |
| Scyphophorus acupunctatus | 120021101110221110000110310110011 |
| Strombocerinae gen. sp. | 110021101110221110000010320000011 |
| Notaris (Erirrhinus) festuca | 101021110110211110000010120000111 |
| Grypus leechi | 101021110110211110000010120000111 |
| Lissorhoptrus simplex | 101021110110211110000010120000111 |
| Stenopelmus rufinasus | 101021101110211110000010120000111 |
| Tanysphyrus lemnae | 100021111110211110000010120000111 |
| Tadius erirhinoides | 101021110110211110000010120100111 |
| Philacta testacea | 100021101110211110000010120000111 |
| Alaocybites sp. | 100021100110211110000010120000??? |
| Gilbertiola sp. | 100021100110211110000010120000??? |
| Schizomicrus caecus | 100021100110211110000010120000??? |
| Perieges bardus | 101021101110211110000010120000??? |
| Antiquis opaque (French amber) | 11?0?11?0110??1?????????????????? |
| Curculio pardalis | 111021111010211110000010120000101 |
| Shigizo sp | 111021110110221120000010120000101 |
| Carponius axillaris | 111021110110221120000010120000101 |
| Timola sp | 111021110110211120000010110100101 |
| Acalyptus carpini | 111021111110211120000010120000101 |
| Amorphoidea lata | 111021111110211122000010320000101 |
| Acentrus histrio | 111021111110211120000010110110101 |
| Anoplus plantaris | 111021111110211120000010110110101 |
| Cionopsis lineola | 111021111110211120000010110110101 |
| Anthonomus fulvus | 111021111110211120000010120000101 |
| Camarotus sp | 111021111110211120000010110110101 |
| Odontopus calceatus | 111021111110211120000010110110101 |
| Ceratopus sp. | 111021111110211120000010110100101 |
| Cionus hortulanus | 110021111110211120000010110110101 |
| Stereonychus fraxini | 111021111110211120000010110110101 |
| Haplonyx scutellatus | 111021110110211120000010110110101 |
| Derelomus basalis | 111021111110211122000010120000101 |
| Phyllotrox (Euclyptus) sp. | 111021111110211120000010320000101 |
| Ellescus ephippiatus | 111021111110211120000010110110101 |
| Dorytomus mucidus | 111021111110211120000010110110101 |
| Sicoderus tinamus | 111021111110211110000010110110101 |
| Ludovix fasciatus | 111021110110211110000010110110101 |
| Rhopalomerus tenuirostris | 111021110110211110000010320000101 |
| Meriphus sp | 111021110110211110000010320000101 |
| Geochus tibialis | 111021101110111120000010120000101 |
| Gymnaetron tetrum | 111021111110211122200001110110101 |
| Myrmex chevrolati | 111021111110211122000010120000101 |

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|---|---|
| Piazorhinus sp. | 111021111110211122000010120000101 |
| Pyropus cyaneus | 111021111010211110000110120000101 |
| Isochnus rufipes | 111021111110211120000010120000101 |
| Tachygonus centralis | 111021111110211120000010120000101 |
| Promecotarsus sp. | 111021111110211120000010120000101 |
| Terires sp. | 111021111110211120000010120000101 |
| Styphlus penicillus | 111021111110211120000010120000101 |
| Tychius picirostris | 111021111110211120000010120000101 |
| Lignyodes horridulus | 111021111110211121000010110000101 |
| Ulomascus parallelus | 111021101010211020000010120010101 |
| Bagous transversus | 100021100110211110001010120000011 |
| Pnigodes setosus | 100021100110211110001010120000011 |
| Hydronomus sinuatocollis | 101021100110211110001010120000011 |
| Baris torquata | 121021111110211122012111110110??? |
| Anthinobaris dispilota | 121021111110211122012111110010??? |
| Limnobaris bicincta | 121021111110211122012111110010??? |
| Torcus nigrinus | 121021111010211122012111110010??? |
| Nicentrus grossulus | 121021110110211122012111110010??? |
| Calandrinus grandicollis | 121021110110111120012010110110??? |
| Eisonyx crassipes | 121021111110111120012010110110??? |
| Pycnobaris pruinosa | 121021111110211122012111310110??? |
| Thanius sp. | 121021111110211122012111110110??? |
| Xystus ater | 121021111110211120012111110110??? |
| Madopterus talpa | 121021111110211122012111110000??? |
| Peridinetus irroratus | 121021111110211122012111110000??? |
| Barinus bivittatus | 121021111110211122012111110110??? |
| Sibariops concurrens | 121021111110211122012111310110??? |
| Diorymeropsis xanthoxyli | 121021111110211122012111110100??? |
| Mononychus punctumalbum | 121021110112211120000000110000??? |
| Pelenomus roelofsi | 121021110112211120000000110000??? |
| Rhinoncus perpendicularis | 121021111112211120000000110000??? |
| Scleropterus serratus | 121021111112211120000000110000??? |
| Rutidosoma globulus | 121021111112211120000000110000??? |
| Homorosoma asperum | 121021111111211120000000110000??? |
| Amalus scortillum | 121021111110211120000000110000??? |
| Ceutorhynchus nitidulus | 121021111112211120000000310000??? |
| Cardipennis sulcithorax | 121021111111211120000000310000??? |
| Dieckmannius sexnotatus | 121021111112211120000000110000??? |
| Coeliodes rana | 121021111112211120000000120000??? |
| Mecysmoderes euglyptus | 121021111111211120000000120000??? |
| Xenysmoderodes sasajii | 121021111110211120000000120000??? |
| Augustinus comes | 121021111111211120000000110000??? |
| Auleutes epilobii | 121021111111211120000000110010??? |
| Cyphosenus citricola | 121021111111211120000000110000??? |
| Anthypurinus haloxylicola | 121021111111211120000000110010??? |
| Lioxyonyx fausti | 121021111110211120000000110010??? |
| Arachnobas gazella | 111021100110211120010000120010001 |
| Campyloscelus westermanni | 111021111110211120010000120010001 |
| Metialma straminea | 111021110110211120000000120010001 |
| Cyllophorus fausciatus | 111021111110211120010000120010001 |
| Acoptus suturalis | 111021111010211120000000120000001 |
| Lobotrachelus troglodytes | 111021111010211120010000120110001 |
| Mecopus trilineatus | 111021110010211120000000120000001 |
| Telephae oculata | 111021110110211120010000120010001 |
| Balanogastris kolae | 111021110110211120010000120100001 |
| Cratosomus "punctulatus" | 111021111010211120000000120000001 |
| Trichodocerus sp. | 111021111010011120000010120000001 |
| Cylindrocopturus operculatus | 111021110110211120000000120000001 |
| Cylindrocopturus adspersus | 111021110110211120000000120000001 |
| Hoplocopturus sp. | 111021110110211120000000120000001 |
| Cossonus impressifrons | 101021111110011120000010110110011 |
| Acamptus echinus | 101021111110011120000010110110011 |

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|---|---|
| Araucarius sp. | 1010211101101111200000101100000011 |
| Catolethrus sp. | 1010211101100111200000101101100011 |
| Pseudopentarthrum atrolucens | 1010211011102111200000101200000011 |
| Macroscytalus chisosensis | 1010211011102111200000101200000011 |
| Proeces depressus | 1010211011102111200000101200000011 |
| Pseudapotrepus sp. | 1010211111101111200000001200000011 |
| Elassoptes marinus | 1010211011102111200000101200000011 |
| Heptarthrum sp. | 1010211011102111200000101200000011 |
| Phloeophagus minor | 1010211011102111200000101200000011 |
| Cryptorhynchus lapathi | 1110211100102111100000102201011101 |
| Coelosternus sp. | 1110211101102111100000102200011101 |
| Eurhoptus sp. | 1110211001102111200000102200011101 |
| Gerstaeckeria lecontei | 1110211002102111200000102200011101 |
| Aedemonus erichsoni | 1110211101102111100000102200011101 |
| Mechistocerus sp. | 1110211111102111100000103100011101 |
| Camptorhinus sp. | 1110211100102111100000103100011101 |
| Cophes obtenus | 1110211110102111100000101200011101 |
| Psepholax humilis | 1110211111102111100000101200011101 |
| Strongylopterus ovatus | 1110211101102111100000101200011101 |
| Torneuma subpanum | 1110211111102111100000101200011101 |
| Bronchus (Hipporhinus) bohemani | 0010201000101111100000101101100??? |
| Amycterus elongata | 0010201001101111100000101101100??? |
| Aegorhinus nodipennis | 0010201101101111000000101101100??? |
| Diabathrarius sp. | 0010211101102111100000101101100??? |
| Gonipterus gibberus | 0010201101102111100000101101100??? |
| Emphyastes fucicola | 0010211001101111200000101101100??? |
| Listroderes costirostris | 0010211100102111100000101101100??? |
| Agraphus bellicus | 0011201011102111100000101101111101 |
| Lepidophorus lineaticolllis | 0011211011102111100000101101001101 |
| Anypotactus jansoni | 0010211000102111100000101200011101 |
| Strophosoma melanogrammus | 0010211000102111100000101200011101 |
| Brachyderes lusitanicus | 0011211000102111100000101200011101 |
| Trigonops platessa | 0011211001102111100000101200101101 |
| Cneorrhinus geminatus | 0011211000102111100000101101111101 |
| Cratopus viridisparsus | 2010211001101111100000101101111101 |
| Cyrtepistomus castanaeus | 2010211001101111100000101101111101 |
| Palirhoeus eatoni | 2011211000101111100000101101111101 |
| Elytrurus griseus | 2011211001101111100000101100111101 |
| Episomus lentus | 2010211002101111100000101200011101 |
| Eudiagogus pulcher | 2010211101101111100000101200011101 |
| Colecerus (Coleocerus) marmoratus | 2010211101101111100000102200111101 |
| Eucoleocerus (Eucolecerus) sp. | 2010211101101111100000101200111101 |
| Eupholus bennetti | 2010211111101111100000101200111101 |
| Compsus argyreus | 2010211101101111100000101101111101 |
| Lachnopus floridanus | 2010211101101111100000101101111101 |
| Hormorus undulatus | 2010211001101111100000102201011101 |
| Leparocerus morio | 2011211001101111100000102200111101 |
| Hypoptus macularis | 2010211001101111100000102200111101 |
| Cyrtomon (Cyphus) lautus | 2010201001101111100000102200111101 |
| Naupactus (Graphognathus) peregrinus | 2010201000112111100000101200111101 |
| Ophryastes (Eupagoderes) argentatus | 2011201000112111100000101200111101 |
| Sciopithes obscurus | 2010211000102111100000101101111101 |
| Pachyrrhynchus tobafolius | 2010211001102111100000102200111101 |
| Stomodes gyrosicollis | 2010211001102111100000101101111101 |
| Rhinospathe albomarginata | 0010201101102111100000101101111101 |
| Liophloeus nubilis | 2010211001102111100000101101111101 |
| Premnotrypes vorax | 2011211001102111100000101101111101 |
| Prypnus scutellaris | 2010201001102111100000101101111101 |
| Rhyncogonus gracilis | 2011211000102111100000101101111101 |
| Mitostylus tenius | 2010211000101111100000101200111101 |
| Sitona californicus | 1010211110102111100000101200000101 |
| Pachnaeus litus | 1010211101102111100000101101111101 |

| | |
|---|---|
| Tanyrhynchus sp. | 201121100010211110000010120011101 |
| Trachyphloeus aristatus | 201121100110211110000010110111101 |
| Rhigopsis effracta | 201121100110211110000010120011101 |
| Dasydema hirtella | 201021110110211110000010120011101 |
| Hypera punctata | 111020100010011110000010010110??? |
| Coniatus tamaricis | 111020110110011110000010010110??? |
| Tylopterus pallidus | 111020100010011110000010020010??? |
| Cepurellus cervinus | 111020100110011110000010020010??? |
| Lixus concavus | 111020110010211110000010120110??? |
| Larinus carlinae | 111021111010211110000010120110??? |
| Apleurus (Dinocleus) molitor | 111021111110211110000010120110??? |
| Stephanocleonus sp. | 111021110110211110000010120110??? |
| Rhinocyllus conicus | 111021110110211110000010120110??? |
| Bangasternus orientalis | 111021110110211110000010120110??? |
| Laemosaccus nephele | 111021101110211112200111121000??? |
| Neolaemosaccus (Saccolaemus) carinicollis | 111021100110211112200111120010??? |
| Magdallis armicollis | 111021100110211112200111120110??? |
| Liparus glabrirostris | 101020110010111120000010130010110 |
| Acicnemis sp. | 121021110110111120000010130010110 |
| Amorphocerus sp. | 111021101110111120000011130000110 |
| Rhyparonotus sp. | 111021100110111110000010120001110 |
| Cholus rana | 111021111110211120000010120111110 |
| Rhyssomatus lineaticollis | 111021110010211120000010120111110 |
| Cleogonus sp. | 121021111010211120000010120111110 |
| Conotrachelus fissunguis | 111021110010211120000010120111110 |
| Gononotus angulicollis | 101021100110211120000010120000110 |
| Guioperus trifasciatus | 101021111010111120000010120001110 |
| Heilus bioculatus | 121021110110111120000010120011110 |
| Heilipodus polygluttatus | 121021110110111120000010110111110 |
| Hylobius pales | 111021110110111120000010110110110 |
| Ithyporus stolidus | 121021110010111020000010110111110 |
| Sclerocardius africanus | 111021110010111020000010110111110 |
| Lepyrus palustris | 111021110110111010000010110111110 |
| Lymantes sandersoni | 101121110110111110000010120001110 |
| Alcidodes dentipes | 111021101010211120000010120010110 |
| Nettarhinus bilobus | 111021110110211110000010120011110 |
| Petalochilus gemellus | 111021110110211110000010120001110 |
| Phrynixus sp. | 201121100110111010000010110111110 |
| Pissodes strobi | 111021110110111110000010120011110 |
| Sternechus paludatus | 121021110110111110000010120000110 |
| Neophycoroetes testaceus | 111021100110111110000010120000110 |
| Trigonocolus curvipes | 121021100010211110000110120010110 |
| Trypetes sp. | 111021110110211120000010120101110 |
| Parorobitus gibbus | 121021110012211120000100120100??? |
| Scolytogenes expers | 110021100000111120001010120010??? |
| Scolytoplatypus tycon | 110021100000111120001010120010??? |
| Xyleborus spathipennis | 101021100000210120001010120010??? |
| Sphaerotrypes pila | 121021100000211110001010110110??? |
| Alniphagus costatus | 110021101000111120001010110110??? |
| Pityophthorus jucundus | 110021101000111120001010110110??? |
| Hylurgops planirostris | 111021100200211120001010120010??? |
| Tesserocerus inermis | 000011101000000120001010120000??? |
| Scolytus multistriatus | 001021110200010110001010120000??? |
| Platypus parallelus | 000021100000000120001010120000??? |
| Ficicis despectus | 000021110200210110001010120000??? |
| Dendroctonus micans | 100021100000210110001010120000??? |
| Diapus aculeatus | 000011100000000110001010120000??? |
| Cylindrobrotus pectinatus (Lebanese amber) | 100021100000210?????????????????? |
| Microborus inertus (Burmese amber) | 100021101200210?????????????????? |
| indet 4 nemonychid (Yixian 2007104 1/2) | ?????????0??????????????????????? |
| indet 3 nemonychid (Yixian 2010159) | ?????????0??????????????????????? |
| indet 2 nemonychid (Yixian 2005111) | ?????????0??????????????????????? |

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Microprobelus liuae (Yixian 2005106)          ?????????0???????????????????????
Microprobelus liuae (Yixian 2007102)          ??00?????0???????????????????????
Chinocimberis augustipecteris (Yixian 2007104) ??00?????0???????????????????????
Chinocimberis augustipecteris (Yixian 2005127) ??00?????0???????????????????????
Chinocimberis magnoculi (Yixian 2010155)      ??00?????0???????????????????????
Chinocimberis magnoculi (Yixian 2005107)      ??00?????0???????????????????????
Chinocimberis augustipecteris (Yixian 2005102) ??00?????0???????????????????????
Renicimberis latipecteris (Yixian 2005123)    ??00?????0???????????????????????
Renicimberis latipecteris (Yixian 2010153)    ??00?????0???????????????????????
Renicimberis latipecteris (Yixian 2005101)    ??00?????0???????????????????????
Renicimberis latipecteris (Yixian 2007101)    ??00?????0???????????????????????
A. concavus (Yixian 2007105)                  ?????????0???????????????????????
A. brachyorhinos (Yixian 2005105)             ???00?11100??????????????????????
A. brachyorhinos (Yixian 2005119)             ?????????0???????????????????????
A. brachyorhinos (Yixian 2005125)             ?????????0???????????????????????
A. macilentus (Yixian 2007103)                ?????????0???????????????????????
A. macilentus (Yixian 2010151)                ?????????0???????????????????????
A. macilentus (Yixian 2010157)                ?????????0???????????????????????
A. macilentus (Yixian 2006102)                ?????????0???????????????????????
A. macilentus (Yixian 2005110 1/2)            ???00?11100??????????????????????
Abrocarina undet. 1 (Yixian 2010154)          ?????????0???????????????????????
A. relicinus (Yixian 2010152)                 ?????????0???????????????????????
A. relicinus (Yixian 2005116 1/2)             ?????????0???????????????????????
A. relicinus (Yixian 2005118)                 ?????????0???????????????????????
A. relicinus (Yixian 2005117)                 ?????????0???????????????????????
A. relicinus (Yixian 2005122)                 ?????????0???????????????????????
A. relicinus (Yixian 2010160)                 ?????????0???????????????????????
A. macilentus (Yixian 2010156)                ?????????0???????????????????????
Archaeorrhynchus acutirostris                 ?????????0???????????????????????
Archaeorrhynchus latitarsus                   ?????????0???????????????????????
Archaeorrhynchus paradoxopus                  ?????????0???????????????????????
Archaeorrhynchus kryzhanovskyi                ?????????0???????????????????????
Archaeorrhynchus nikolaevi                    ?????????0???????????????????????
Archaeorrhynchus carpenteri                   ?????????0???????????????????????
Archaeorrhynchus sukatshevai                  ?????????0???????????????????????
Archaeorrhynchoides crowsoni                  ?????????0???????????????????????
Archaeorrhynchoides arnoldii                  ?????????0???????????????????????
Kararhynchus occiduus                         ?????????0???????????????????????
Eobelus longipes                              ?????????0???????????????????????
Eobelus sp.                                   ?????????0???????????????????????
Belonotaris karatavicus                       ?????????0???????????????????????
Probelus tibialis                             ?????????0???????????????????????
Probelus cockerelli                           ?????????0???????????????????????
Probelus scudderi                             ?????????0???????????????????????
Probelus longitarsus                          ?????????0???????????????????????
Probelus curvispinus                          ?????????0???????????????????????
Probelus handlirschi                          ?????????0???????????????????????
Probelopsis acutiapex                         ?????????0???????????????????????
Arnoldibelus wanatavieus                      ?????????0???????????????????????
Arnoldibelus gratshevi                        ?????????0???????????????????????
Arnoldibelus zherichini                       ?????????0???????????????????????
Arnoldibelus medvedevi                        ?????????0???????????????????????
Arnoldibelus rasnitsyni                       ?????????0???????????????????????
Arnoldibelus rohdendorfi                      ?????????0???????????????????????
Arnoldibelus wickhami                         ?????????0???????????????????????
Arnoldibelus korotyaevi                       ?????????0???????????????????????
Arnoldibelus heeri                            ?????????0???????????????????????
Arnoldibelus martynovi                        ?????????0???????????????????????
Arnoldibelus karatavicus                      ?????????0???????????????????????
Nanophydes ovatus                             ?????????0???????????????????????
Ampliceps dentitibia                          ?????????0???????????????????????
Ampliceps furcitibia                          ?????????0???????????????????????
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| | |
|---|---|
| Oxycorynoides progressivus | ?????????0??????????????????????? |
| Karataucarodes zimmermanni | ?????????0??????????????????????? |
| Scelocamptus dubius | ?????????0??????????????????????? |
| Scelocamptus curvipes | ?????????0??????????????????????? |
| Oxycorynoides rohdendorfi | ?????????0??????????????????????? |
| Oxycorynoides brevipes | ?????????0??????????????????????? |
| Oxycorynoides zherichini | ?????????0??????????????????????? |
| Oxycorynoides similis | ?????????0??????????????????????? |
| Belonartis lineatipunctatus | ?????????0??????????????????????? |
| Oxycorynoides mongolicus | ?????????0??????????????????????? |
| Oxycorynoides gurvanensis | ?????????0??????????????????????? |
| Eccoptarthroides longirostris | ?????????0??????????????????????? |
| Eccoptarthroides ponomarenkoi | ?????????0??????????????????????? |
| Eccoptarthroides martynovi | ?????????0??????????????????????? |
| Eccoptarthroides nikitskyi | ?????????0??????????????????????? |
| Pseudobrenthorrhinus magnus | ?????????0??????????????????????? |
| Pseudobrenthorrhinus crassicornis | ?????????0??????????????????????? |
| Brenthorrhinus mirabilis | ?????????0??????????????????????? |
| Gobibrenthorrhinus gigas | ?????????0??????????????????????? |
| Brenthorrhinus brevirostris | ?????????0??????????????????????? |
| Brenthorrhinoides mandibulatus | ?????????0??????????????????????? |
| Scelocamptus tenuirostris | ?????????0??????????????????????? |
| Brenthorrhinoides robustus | ?????????0??????????????????????? |
| Brenthorrhinoides pubescens | ?????????0??????????????????????? |
| Mongolbrenthorrhinus arnoldii | ?????????0??????????????????????? |
| Mongolbrenthorrhinus pusillus | ?????????0??????????????????????? |
| Mongolbrenthorrhinus flavus | ?????????0??????????????????????? |
| Testudobrenthorrhinus baissiensis | ?????????0??????????????????????? |
| Testudobrenthorrhinus taetricus | ?????????0??????????????????????? |
| Buryatnemonyx niger | ?????????0??????????????????????? |
| Buryatnemonyx tener | ?????????0??????????????????????? |
| Buryatnemonyx gratshevi | ?????????0??????????????????????? |
| Oxycorynoides ponomarenkoi | ?????????0??????????????????????? |
| Procurculio fortipes | ?????????0??????????????????????? |
| Procurculio pallens | ?????????0??????????????????????? |
| Megabrenthorrhinus grandis | ?????????0??????????????????????? |
| Megabrenthorrhinus longicornis | ?????????0??????????????????????? |
| Eccoptarthrus crassipes | ?????????0??????????????????????? |
| Eccoptothorax latipennis | ?????????0??????????????????????? |
| Distenorrhinus pallidirostris | ?????????0??????????????????????? |
| Distenorrhinus ovatus | ?????????0??????????????????????? |
| Distenorrhinus arnoldii | ?????????0??????????????????????? |
| Distenorrhinus elongatus | ?????????0??????????????????????? |
| Distenorrhinus rotundicollis | ?????????0??????????????????????? |
| Distenorrhinus angulatus | ?????????0??????????????????????? |
| Distenorrhinus major | ?????????0??????????????????????? |
| Distenorrhinus antennatus | ?????????0??????????????????????? |
| Paroxycorynoides elegans | ?????????0??????????????????????? |
| Selengarhynchoides sharyngolensis | ?????????0??????????????????????? |
| Selengarhynchus ovalis | ?????????0??????????????????????? |
| Pseudonemonyx stupendus | ?????????0??????????????????????? |
| Cretonemonyx minimus | ?????????0??????????????????????? |
| Cretonemonyx longirostris | ?????????0??????????????????????? |
| Cretonemonyx profligatus | ?????????0??????????????????????? |
| Megametrioxenoides longus | ?????????0??????????????????????? |
| Megametrioxenoides proelomus | ?????????0??????????????????????? |
| Cretoxenoides erdeniensis | ?????????0??????????????????????? |
| Chinocimberis dispersus | ?????????0??????????????????????? |
| Baissimberis prodigiosus | ?????????0??????????????????????? |
| Mongolocar orcinus (nemonychid) | ?????????0??????????????????????? |
| Karacar contractus (nemonychid) | ?????????0??????????????????????? |
| Baissabrenthorrhinus mirabilis | ?????????0??????????????????????? |

| | |
|---|---|
| Ulyaniana nobilis | ??0?????10??0???????????????????? |
| Ulyaniana excellens | ??0?????10??0???????????????????? |
| Ulyanisca dentipes | ??0?????10??0???????????????????? |
| Slonik sibiricus | ??0?????10??????????????????????? |
| Hyperites nadezhkini | ??0?????10??????????????????????? |

TABLE 9. Characters 264 - 281

| | 264 269 274 279 |
|---|---|
| Cucujus clavipes | 100000011001000011 |
| Orsodacne atra childreni (Orsodacnidae) | 100001010001000011 |
| Fidia viticida (Chrysomelidae) | 100111000003000011 |
| Cimberis sp. | 100101010000000001 |
| Nannomacer germaini | 100111010010000001 |
| Mecomacer scambus | 100111010010000001 |
| Rhynchitomacerinus kuscheli | 100111010010000001 |
| Nemonyx lepturoides | 100101010000000001 |
| Doydirhynchus austriacus | 100101010000000001 |
| Lecontellus byturoides | 100101010000000001 |
| Arra similis (Spanish amber) | ????01????????0001 |
| indet 5 anthribid (Yixian 2005126) | ?????????????????? |
| Trigonorhinus sp. | 100111001112000001 |
| Anthribus nebulosus | 100111001112000001 |
| Epicerastes sp. | 100111000112000001 |
| Apolecta samarana | 100111001112000001 |
| Gynandrocerus sp. | 100111011112000001 |
| Phaenithon semigriseum | 100111000112000001 |
| Basitropis sp. | 100111000112000001 |
| Strabus bimaculatus | 100111000112000001 |
| Corrhecerus sp | 100111000112000001 |
| Straboscopus tessellatus | 100111001112000001 |
| Euparius marmoreus | 100111000112000001 |
| Discotenes nigrotuberculata | 100111000112000001 |
| Ischnocerus infuscatus | 100111000112000001 |
| Dendropemon sp. | 100111000112000001 |
| Eucorynus crassicornis | 100111000112000001 |
| Gymnognathus sp. | 100111000112000001 |
| Dinema filicornis | 100111000012000001 |
| Neseonos brunneus | 100111000012000001 |
| Mauia subnotata | 100111000012000001 |
| Illis anna | 100111000012000001 |
| Mecocerus sp. | 100111000112000001 |
| Acanthothorax basalis | 100111000112000001 |
| Phloeophilus sulcifrons | 100111000112000001 |
| Mycetis marginicollis | 100111000012000001 |
| Ormiscus sp. | 100111000112000001 |
| Ozotomerus bipunctatus | 100111000113000001 |
| Piesocorynus sellatus | 100111000112000001 |
| Brachycorynus distentus | 100111000112000001 |
| Goniocloeus sp. | 100111000112000001 |
| Platyrhinus resinosus | 100111000113000001 |
| Phoenicobiella chamaeropis | 100111000112000001 |
| Toxonotus fascicularis | 100111000112000001 |
| Phloeobius pallipes | 100111000112000001 |
| Platystomos wallacei | 100111000113000001 |
| Ptychoderes sp. | 100111000112000001 |
| Phloeotragus polyopras | 100111000112000001 |
| Cerambyrhynchus schoenherri | 100111000112000001 |
| Rhinotropis superciliaris | 100111000112000001 |
| Sintor quadrilineatus | 100111000112000001 |
| Allandrus bifasciatus | 100111000112000001 |

| | |
|---|---|
| Stenocerus sp. | 100111000112000001 |
| Plintheria plintheroides | 100111000112000001 |
| Trigonorhinus sticticus | 100111000112000001 |
| Tropideres fasciatus | 100111000112000001 |
| Acorynus pallipes | 100111000113000001 |
| Cedus guttatus | 100111000112000001 |
| Xenocerus ancyra | 100111000112000001 |
| Xylinada rugicollis | 100111000112000001 |
| Stiboderes westermanni | 100111000112000001 |
| Exechesops bakeri | 100111000112000001 |
| Holostilpna sp. | 100111000112000001 |
| Choragus sayi | 100111000112000001 |
| Euxenus jordani | 100111000112000001 |
| Araecerus levipennis | 100111000112000001 |
| Acaromimus americanus | 100101000112000001 |
| Misthosima sp. | 100111000112000001 |
| Cisanthribus sp. | 100101000112000001 |
| Notioxenus ater | 100111000112000001 |
| Urodon rufipes | 100111000113000001 |
| Rhinotia sp. | 101001000201000011 |
| Belus semipunctatus | 101001000201000011 |
| Homalocerus lyciformis | 101001000201000011 |
| Pachyura australis | 001001000201000111 |
| Dicordylus marmoratus | 001001000001000111 |
| Daohugou belid sp. | ????0?????????0??1 |
| Montsecbelus solutus | ???????0??????0??? |
| Car sp. | 0110010020000000?1 |
| Car condensatus | 0110010020000000?1 |
| Caenominurus topali | 0110010020000000?1 |
| Albicar contriti (Spanish amber) | ????0??020????0??1 |
| Chilecar pilgerodendri | 0110010020000000?1 |
| Carodes revelatus | 01100100?0000000?1 |
| Baissorhynchus tarsalis | ???????0??????0??? |
| Paleocar princeps | ???????0??????0??? |
| Baissacar passarius | ???????0??????0??? |
| Cretonanophyes longirostris | ????0??0??????0??1 |
| Cretonanophyes punctatus | ????0??0??????0??1 |
| C. punctatus (Yixian 2007105 1/2) | ?????????????????? |
| C. punctatus (Yixian 2006103) | ?????????????????? |
| C. punctatus (Yixian 2005115) | ?????????????????? |
| C. punctatus (Yixian 2010158) | ?????????????????? |
| C. zherikhini (Yixian 2006101) | ?????????????????? |
| C. zherikhini (Yixian 2005113) | ?????????????????? |
| C. zherikhini (Yixian 2005114) | ?????????????????? |
| C. zherikhini (Yixian 2005109) | ?????????????????? |
| C. zherikhini (Yixian 2005112) | ?????????????????? |
| C. zherikhini (Yixian 2005103) | ?????????????????? |
| Cretonanophyes asiaticus (sp1) | ????0??0??????0??1 |
| Cretonanophyes neocomicus (sp2) | ????0??0??????0??1 |
| Jarzembowskia edmundi | ?????????????????? |
| Baissacarodes sibiricus | ??????????????0??? |
| Emanrhynchus lebedevi | ??????????????0??? |
| Gobicar ponomarenkoi | ??????????????0??? |
| Gobicar ulugeiensis | ??????????????0??? |
| Mesophyletis calhouni | ???????0??????0??1 |
| Hispanocar kseniae | ?????????????????? |
| Martinsnetoa dubia | ???????0??????0??? |
| Cretocar luzzii | ????0??0?0????0??1 |
| Montsecanomalus zherikhini | ??????????????0??? |
| Zigras cornus | ????0??0?0????0??1 |
| Zigras nudicornus | ????0??0?0????0??1 |
| Scabridus implexus | ????0??0??????0??1 |

| | |
|---|---|
| Scabridus zigrasi | ????0??0??????0??1 |
| Anchineus dolichobothris | ???????0??????0??? |
| Caridae 1 | ???????0??????0??1 |
| Caridae 2 | ???????0??????0??1 |
| Caridae 3 | ???????0??????0??1 |
| Preclarusbelus vanini | ??????????????0??? |
|Arariperhinus monnei | ?????????????????? |
| Gratshevbelus erici | ??????????????0??? |
| Proterhinus sp. | 101001002101000111 |
| Rhopalotria bicolor | 101001002101000111 |
| Parallocorynus bicolor | 101001001101000111 |
| Baltocar succinicus | ????1??0??????0??1 |
| Haplorhynchites aeneus | 000001001000000001 |
| Involvulus hirtus | 000001001000000001 |
| Merhynchites bicolor | 000011001000000001 |
| Eugnamptus punctatus | 000011001000000001 |
| Auletobius cassandrae | 000001001000000001 |
| Minurus testaceus | 000001001000000001 |
| Pseudauletes sp. | 000001001000000001 |
| Byctiscus populi | 000001001000000001 |
| Listrobytiscus corvinus coeruleipennis | 000001001000000001 |
| Deporaus glastinus | 000001001000000001 |
| Pterocolus ovatus | 000011001000000001 |
| Homeolabus analis | 000111001000000001 |
| Attelabus nigripes | 000111001000000001 |
| Omolabus conicollis | 000111001000000001 |
| Euscelus dentipes | 000111001000000001 |
| Henicolabus octospilotus | 000111001000000001 |
| Lamprolabus sandacanus | 000111001000000001 |
| Euops quadrifasciculatus | 000111001000000001 |
| Pilolabus viridans | 000111001000000001 |
| Apoderus sp. | 000101001000000001 |
| Parapoderus flavoebenus | 000101001000000001 |
| Clitostylus badeni | 000101001000000001 |
| Holapoderus hystrix | 000101001000000001 |
| Paroplapoderus pardalis | 000101001000000001 |
| Cynotrachelus roelofsi | 000101001000000001 |
| Trachelophorus giraffa | 000101001000000001 |
| Ithycerus noveboracensis | 111101001001000010 |
| Brentus anchorago | 011101001000000010 |
| Arrhenodes minutus | 011101001000000010 |
| Henarrhenodes macgregori | 011101001000000010 |
| Baryrrhynchus schroderi | 011101001000000010 |
| Amorphocephala imitator | 011101001000000010 |
| Antliarhinites zamiae | 011101001000000010 |
| Cylas formicarius elegantulus | 011101001000000010 |
| Oncodemerus sennai | 011101001000000010 |
| Stereodermus latirostris | 011101001000000010 |
| Cerobates sexsulcatus | 011101001000000010 |
| Taphroderopsis oscillator | 011101001000000010 |
| Paratrachelizus uncimanus | 011101001000000010 |
| Miolispa robusta | 011101001000000010 |
| Nemocephalus guatemalensis | 011101001000000010 |
| Diuris shelfordi | 011101001000000010 |
| Ithystenus hollandiae | 011101001000000010 |
| Schizotrachelus bakeri | 011101001000000010 |
| Hormocerus scrobicollis | 011101001000000010 |
| Ulocerus sp. | 011101001000000010 |
| Aporhina sp. | 111101001001000010 |
| Apion longirostre | 011001001001000010 |
| Sayapion arizona | 011001001001000010 |
| Perapion punctinasum | 011001001001000010 |

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|---|---|
| Phrissotrichum tubiferum | 011001001001000010 |
| Alocentron attenuatum | 011001001001000010 |
| Aspidapion radiolus | 011001001001000010 |
| Ceratapion basicorne | 011001001001000010 |
| Omphalapion hookeri | 011001001001000010 |
| Cybebus dimidiatus | 011001001001000010 |
| Exapion ulicis | 011001001001000010 |
| Ixapion herculanum | 011001001001000010 |
| Kalcapion flavofemoratum | 011001001001000010 |
| Melanapion minimum | 011001001001000010 |
| Malvapion malvae | 011001001001000010 |
| Rhopalapion longirostre | 011001001001000010 |
| Noterapion meorrhynchum | 011001001001000010 |
| Eutrichapion alakanum | 011001001001000010 |
| Capapion seniculus | 011001001001000010 |
| Stenopterapion tenue | 011001001001000010 |
| Trichapion gracilirostre | 011001001001000010 |
| Chrysapion auctum | 011001001001000010 |
| Protapion apricans | 011001001001000010 |
| Tanaos bicolor | 011001001001000010 |
| Nanophyes canadensis | 011001001001000010 |
| Dieckmanniellus nitidulus | 011001001001000010 |
| Corimalia tamarisei | 011001001001000010 |
| Allomalia quadrivirgata | 011001001001000010 |
| Bracycerus sp. | 011101001001000010 |
| Microcerus costalis | 011101001001000010 |
| Episus gibbosus | 011101001001000010 |
| Ocladius obliquesetosus | 011101001001000010 |
| Desmidophorus sp. | 011101001001000010 |
| Dryophthorus americanus | 110101011001101110 |
| Stenommatus sulcifrons | 110101011001101110 |
| Cryptoderma sp. | 110101011002120110 |
| Orthognathus subparallelus | 110101011001101110 |
| Mesocordylus bracteolatus | 110101011001101110 |
| Yuccaborus frontalis | 110101011002101110 |
| Rhinostomus thompsoni | 110101011002101110 |
| Rhynchophorus palmarum | 110101011002101110 |
| Otidognathus sp | 110101011002101110 |
| Diocalandra frumenti | 110101011002101110 |
| Toxorhinus baonii | 110101011002121110 |
| Sitophilus oryzae | 110101011002121110 |
| Aphiocephalus guerini | 110101011002101110 |
| Ommatolampus paratasioides | 110101011002101110 |
| Polytus mellerborgii | 110101011002121110 |
| Rhodobaenus tredecimpunctatus | 110101011002121110 |
| Scyphophorus acupunctatus | 110101011002121110 |
| Strombocerinae gen. sp. | 110101001002021110 |
| Notaris (Erirrhinus) festuca | 111001001001001010 |
| Grypus leechi | 111001001001001010 |
| Lissorhoptrus simplex | 111001001001001010 |
| Stenopelmus rufinasus | 111001001001001010 |
| Tanysphyrus lemnae | 111001001001001010 |
| Tadius erirhinoides | 111001001003001010 |
| Philacta testacea | 111001001003001010 |
| Alaocybites sp. | ????01001003001010 |
| Gilbertiola sp. | ????01001003001010 |
| Schizomicrus caecus | ????01001003001010 |
| Perieges bardus | ????01001001000010 |
| Antiquis opaque (French amber) | ????0????0????1??0 |
| Curculio pardalis | 011001001004021110 |
| Shigizo sp | 011001001004021110 |
| Carponius axillaris | 011001001004021110 |

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|---|---|
| Timola sp | 011001001004021110 |
| Acalyptus carpini | 011001001004021110 |
| Amorphoidea lata | 011001001004021110 |
| Acentrus histrio | 011001001004021110 |
| Anoplus plantaris | 011001001004021110 |
| Cionopsis lineola | 011001001004021110 |
| Anthonomus fulvus | 011001001004021110 |
| Camarotus sp | 011001001004021110 |
| Odontopus calceatus | 011001001004021110 |
| Ceratopus sp. | 011001001004021110 |
| Cionus hortulanus | 011001001004021110 |
| Stereonychus fraxini | 011001001004021110 |
| Haplonyx scutellatus | 011001001004021110 |
| Derelomus basalis | 011001001004021110 |
| Phyllotrox (Euclyptus) sp. | 011001001004021110 |
| Ellescus ephippiatus | 011001001004021110 |
| Dorytomus mucidus | 011001001004021110 |
| Sicoderus tinamus | 011001001004021110 |
| Ludovix fasciatus | 011001001004021110 |
| Rhopalomerus tenuirostris | 011001001004021110 |
| Meriphus sp | 011001001004021110 |
| Geochus tibialis | 011001001004021110 |
| Gymnaetron tetrum | 011001001004021110 |
| Myrmex chevrolati | 011001001004021110 |
| Piazorhinus sp. | 011001001004021110 |
| Pyropus cyaneus | 011001001004021110 |
| Isochnus rufipes | 011001001004021110 |
| Tachygonus centralis | 011001001004021110 |
| Promecotarsus sp. | 011001001004021110 |
| Terires sp. | 011001001004021110 |
| Styphlus penicillus | 011001001004021110 |
| Tychius picirostris | 011001001004021110 |
| Lignyodes horridulus | 011001001004021110 |
| Ulomascus parallelus | 011001001004021110 |
| Bagous transversus | 101001001003001110 |
| Pnigodes setosus | 101001001003001110 |
| Hydronomus sinuatocollis | 101001001002001110 |
| Baris torquata | ????01001004021110 |
| Anthinobaris dispilota | ????01001004021110 |
| Limnobaris bicincta | ????01001004021110 |
| Torcus nigrinus | ????01001004021110 |
| Nicentrus grossulus | ????01001004021110 |
| Calandrinus grandicollis | ????01001004021110 |
| Eisonyx crassipes | ????01001004021110 |
| Pycnobaris pruinosa | ????01001004021110 |
| Thanius sp. | ????01001004021110 |
| Xystus ater | ????01001004021110 |
| Madopterus talpa | ????01001004021110 |
| Peridinetus irroratus | ????01001004021110 |
| Barinus bivittatus | ????01001004021110 |
| Sibariops concurrens | ????01001004021110 |
| Diorymeropsis xanthoxyli | ????01001004021110 |
| Mononychus punctumalbum | ????01001004021110 |
| Pelenomus roelofsi | ????01001004021110 |
| Rhinoncus perpendicularis | ????01001004021110 |
| Scleropterus serratus | ????01001004021110 |
| Rutidosoma globulus | ????01001004021110 |
| Homorosoma asperum | ????01001004021110 |
| Amalus scortillum | ????01001004021110 |
| Ceutorhynchus nitidulus | ????01001004021110 |
| Cardipennis sulcithorax | ????01001004021110 |
| Dieckmannius sexnotatus | ????01001004021110 |

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|---|---|
| Coeliodes rana | ????01001004021110 |
| Mecysmoderes euglyptus | ????01001004021110 |
| Xenysmoderodes sasajii | ????01001004021110 |
| Augustinus comes | ????01001004021110 |
| Auleutes epilobii | ????01001004021110 |
| Cyphosenus citricola | ????01001004021110 |
| Anthypurinus haloxylicola | ????01001004021110 |
| Lioxyonyx fausti | ????01001004021110 |
| Arachnobas gazella | 011101001004021110 |
| Campyloscelus westermanni | 011101001004021110 |
| Metialma straminea | 011101001004021110 |
| Cyllophorus fausciatus | 011101001004021110 |
| Acoptus suturalis | 011101001004021110 |
| Lobotrachelus troglodytes | 011101001004021110 |
| Mecopus trilineatus | 011101001004021110 |
| Telephae oculata | 011101001004021110 |
| Balanogastris kolae | 011101001004021110 |
| Cratosomus "punctulatus" | 011101001004021110 |
| Trichodocerus sp. | 011101001004021110 |
| Cylindrocopturus operculatus | 011101001004021110 |
| Cylindrocopturus adspersus | 011101001004021110 |
| Hoplocopturus sp. | 011101001004021110 |
| Cossonus impressifrons | 011001001004021110 |
| Acamptus echinus | 011001001004021110 |
| Araucarius sp. | 011001001004021110 |
| Catolethrus sp. | 011001001004021110 |
| Pseudopentarthrum atrolucens | 011001001004021110 |
| Macroscytalus chisosensis | 011001001004021110 |
| Proeces depressus | 011001001004021110 |
| Pseudapotrepus sp. | 011001001004021110 |
| Elassoptes marinus | 011001001004021110 |
| Heptarthrum sp. | 011001001004021110 |
| Phloeophagus minor | 011001001004021110 |
| Cryptorhynchus lapathi | 011101001004021110 |
| Coelosternus sp. | 011101001004021110 |
| Eurhoptus sp. | 011101001004021110 |
| Gerstaeckeria lecontei | 011101001004021110 |
| Aedemonus erichsoni | 011101001004021110 |
| Mechistocerus sp. | 011101001004021110 |
| Camptorhinus sp. | 011101001004021110 |
| Cophes obtenus | 011101001004021110 |
| Psepholax humilis | 011101001004021110 |
| Strongylopterus ovatus | 011101001004021110 |
| Torneuma subpanum | 011101001004021110 |
| Bronchus (Hipporhinus) bohemani | ????01001004021110 |
| Amycterus elongata | ????01001004021110 |
| Aegorhinus nodipennis | ????01001004021110 |
| Diabathrarius sp. | ????01001004021110 |
| Gonipterus gibberus | ????01001004021110 |
| Emphyastes fucicola | ????01001004021110 |
| Listroderes costirostris | ????01001004021110 |
| Agraphus bellicus | 011001001004021110 |
| Lepidophorus lineaticolllis | 011001001004021110 |
| Anypotactus jansoni | 011001001004021110 |
| Strophosoma melanogrammus | 011001001004021110 |
| Brachyderes lusitanicus | 011001001004021110 |
| Trigonops platessa | 011001001004021110 |
| Cneorrhinus geminatus | 011001001004021110 |
| Cratopus viridisparsus | 011001001004021110 |
| Cyrtepistomus castanaeus | 011001001004021110 |
| Palirhoeus eatoni | 011001001004021110 |
| Elytrurus griseus | 011001001004021110 |

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|---|---|
| Episomus lentus | 01100100100402111O |
| Eudiagogus pulcher | 011001001004021110 |
| Colecerus (Coleocerus) marmoratus | 011001001004021110 |
| Eucoleocerus (Eucolecerus) sp. | 011001001004021110 |
| Eupholus bennetti | 011001001004021110 |
| Compsus argyreus | 011001001004021110 |
| Lachnopus floridanus | 011001001004021110 |
| Hormorus undulatus | 011001001004021110 |
| Leparocerus morio | 011001001004021110 |
| Hypoptus macularis | 011001001004021110 |
| Cyrtomon (Cyphus) lautus | 011001001004021110 |
| Naupactus (Graphognathus) peregrinus | 011001001004021110 |
| Ophryastes (Eupagoderes) argentatus | 011001001004021110 |
| Sciopithes obscurus | 011001001004021110 |
| Pachyrrhynchus tobafolius | 011001001004021110 |
| Stomodes gyrosicollis | 011001001004021110 |
| Rhinospathe albomarginata | 011001001004021110 |
| Liophloeus nubilis | 011001001004021110 |
| Premnotrypes vorax | 011001001004021110 |
| Prypnus scutellaris | 011001001004021110 |
| Rhyncogonus gracilis | 011001001004021110 |
| Mitostylus tenius | 011001001004021110 |
| Sitona californicus | 011001001004021110 |
| Pachnaeus litus | 011001001004021110 |
| Tanyrhynchus sp. | 011001001004021110 |
| Trachyphloeus aristatus | 011001001004021110 |
| Rhigopsis effracta | 011001001004021110 |
| Dasydema hirtella | 011001001004021110 |
| Hypera punctata | ????01001004021110 |
| Coniatus tamaricis | ????01001004021110 |
| Tylopterus pallidus | ????01001004021110 |
| Cepurellus cervinus | ????01001004021110 |
| Lixus concavus | ????01001004021110 |
| Larinus carlinae | ????01001004021110 |
| Apleurus (Dinocleus) molitor | ????01001004021110 |
| Stephanocleonus sp. | ????01001004021110 |
| Rhinocyllus conicus | ????01001004021110 |
| Bangasternus orientalis | ????01001004021110 |
| Laemosaccus nephele | ????01001004021110 |
| Neolaemosaccus (Saccolaemus) carinicollis | ????01001004021110 |
| Magdallis armicollis | ????01001004021110 |
| Liparus glabrirostris | 011101001004021110 |
| Acicnemis sp. | 011101001004021110 |
| Amorphocerus sp. | 011101001004021110 |
| Rhyparonotus sp. | 011101001004021110 |
| Cholus rana | 011101001004021110 |
| Rhyssomatus lineaticollis | 011101001004021110 |
| Cleogonus sp. | 011101001004021110 |
| Conotrachelus fissunguis | 011101001004021110 |
| Gononotus angulicollis | 011101001004021110 |
| Guioperus trifasciatus | 011101001004021110 |
| Heilus bioculatus | 011101001004021110 |
| Heilipodus polygluttatus | 011101001004021110 |
| Hylobius pales | 011101001004021110 |
| Ithyporus stolidus | 011101001004021110 |
| Sclerocardius africanus | 011101001004021110 |
| Lepyrus palustris | 011101001004021110 |
| Lymantes sandersoni | 011101001004021110 |
| Alcidodes dentipes | 011101001004021110 |
| Nettarhinus bilobus | 011101001004021110 |
| Petalochilus gemellus | 011101001004021110 |
| Phrynixus sp. | 011101001004021110 |

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|---|---|
| Pissodes strobi | 011101001004021110 |
| Sternechus paludatus | 011101001004021110 |
| Neophycoroetes testaceus | 011100001004021110 |
| Trigonocolus curvipes | 011101101004021110 |
| Trypetes sp. | 011101101004021110 |
| Parorobitus gibbus | ????01001004021110 |
| Scolytogenes expers | ????01110113000011 |
| Scolytoplatypus tycon | ????01110113000011 |
| Xyleborus spathipennis | ????00110013000110 |
| Sphaerotrypes pila | ????00110113000001 |
| Alniphagus costatus | ????00010113000001 |
| Pityophthorus jucundus | ????00110113000110 |
| Hylurgops planirostris | ????01010113000000 |
| Tesserocerus inermis | ????01010113000110 |
| Scolytus multistriatus | ????01010113000011 |
| Platypus parallelus | ????01010113000110 |
| Ficicis despectus | ????01010113000110 |
| Dendroctonus micans | ????01110113000110 |
| Diapus aculeatus | ????01010113000110 |
| Cylindrobrotus pectinatus (Lebanese amber) | ????0?010?1???0??1 |
| Microborus inertus (Burmese amber) | ????0?010?1???0??1 |
| indet 4 nemonychid (Yixian 2007104 1/2) | ??????????????0??1 |
| indet 3 nemonychid (Yixian 2010159) | ??????????????0??1 |
| indet 2 nemonychid (Yixian 2005111) | ??????????????0??1 |
| Microprobelus liuae (Yixian 2005106) | ??????????????0??1 |
| Microprobelus liuae (Yixian 2007102) | ??????????????0??1 |
| Chinocimberis augustipecteris (Yixian 2007104) | ???????1??????0??1 |
| Chinocimberis augustipecteris (Yixian 2005127) | ???????1??????0??1 |
| Chinocimberis magnoculi (Yixian 2010155) | ???????1??????0??1 |
| Chinocimberis magnoculi (Yixian 2005107) | ???????1??????0??1 |
| Chinocimberis augustipecteris (Yixian 2005102) | ???????1??????0??1 |
| Renicimberis latipecteris (Yixian 2005123) | ???????1??????0??1 |
| Renicimberis latipecteris (Yixian 2010153) | ???????1??????0??1 |
| Renicimberis latipecteris (Yixian 2005101) | ???????1??????0??1 |
| Renicimberis latipecteris (Yixian 2007101) | ???????1??????0??1 |
| A. concavus (Yixian 2007105) | ????0?????????0??1 |
| A. brachyorhinos (Yixian 2005105) | ????0??1??????0??1 |
| A. brachyorhinos (Yixian 2005119) | ????0?????????0??1 |
| A. brachyorhinos (Yixian 2005125) | ????0?????????0??1 |
| A. macilentus (Yixian 2007103) | ????0?????????0??1 |
| A. macilentus (Yixian 2010151) | ????0?????????0??1 |
| A. macilentus (Yixian 2010157) | ????0?????????0??1 |
| A. macilentus (Yixian 2006102) | ????0?????????0??1 |
| A. macilentus (Yixian 2005110 1/2) | ????0??1??????0??1 |
| Abrocarina undet. 1 (Yixian 2010154) | ????0?????????0??1 |
| A. relicinus (Yixian 2010152) | ????0?????????0??1 |
| A. relicinus (Yixian 2005116 1/2) | ????0?????????0??1 |
| A. relicinus (Yixian 2005118) | ????0?????????0??1 |
| A. relicinus (Yixian 2005117) | ????0?????????0??1 |
| A. relicinus (Yixian 2005122) | ????0?????????0??1 |
| A. relicinus (Yixian 2010160) | ????0?????????0??1 |
| A. macilentus (Yixian 2010156) | ????0?????????0??1 |
| Archaeorrhynchus acutirostris | ??????????????0??1 |
| Archaeorrhynchus latitarsus | ??????????????0??1 |
| Archaeorrhynchus paradoxopus | ??????????????0??1 |
| Archaeorrhynchus kryzhanovskyi | ??????????????0??1 |
| Archaeorrhynchus nikolaevi | ??????????????0??1 |
| Archaeorrhynchus carpenteri | ??????????????0??1 |
| Archaeorrhynchus sukatshevai | ??????????????0??1 |
| Archaeorrhynchoides crowsoni | ??????????????0??1 |
| Archaeorrhynchoides arnoldii | ??????????????0??1 |
| Kararhynchus occiduus | ??????????????0??1 |

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|---|---|
| Eobelus longipes | ??????????????0??1 |
| Eobelus sp. | ??????????????0??1 |
| Belonotaris karatavicus | ??????????????0??1 |
| Probelus tibialis | ??????????????0??1 |
| Probelus cockerelli | ??????????????0??1 |
| Probelus scudderi | ??????????????0??1 |
| Probelus longitarsus | ??????????????0??1 |
| Probelus curvispinus | ??????????????0??1 |
| Probelus handlirschi | ??????????????0??1 |
| Probelopsis acutiapex | ??????????????0??1 |
| Arnoldibelus wanatavieus | ??????????????0??1 |
| Arnoldibelus gratshevi | ??????????????0??1 |
| Arnoldibelus zherichini | ??????????????0??1 |
| Arnoldibelus medvedevi | ??????????????0??1 |
| Arnoldibelus rasnitsyni | ??????????????0??1 |
| Arnoldibelus rohdendorfi | ??????????????0??1 |
| Arnoldibelus wickhami | ??????????????0??1 |
| Arnoldibelus korotyaevi | ??????????????0??1 |
| Arnoldibelus heeri | ??????????????0??1 |
| Arnoldibelus martynovi | ??????????????0??1 |
| Arnoldibelus karatavicus | ??????????????0??1 |
| Nanophydes ovatus | ??????????????0??1 |
| Ampliceps dentitibia | ??????????????0??1 |
| Ampliceps furcitibia | ??????????????0??1 |
| Oxycorynoides progressivus | ??????????????0??1 |
| Karataucarodes zimmermanni | ??????????????0??1 |
| Scelocamptus dubius | ??????????????0??1 |
| Scelocamptus curvipes | ??????????????0??1 |
| Oxycorynoides rohdendorfi | ??????????????0??1 |
| Oxycorynoides brevipes | ??????????????0??1 |
| Oxycorynoides zherichini | ??????????????0??1 |
| Oxycorynoides similis | ??????????????0??1 |
| Belonartis lineatipunctatus | ??????????????0??1 |
| Oxycorynoides mongolicus | ??????????????0??1 |
| Oxycorynoides gurvanensis | ??????????????0??1 |
| Eccoptarthroides longirostris | ??????????????0??1 |
| Eccoptarthroides ponomarenkoi | ??????????????0??1 |
| Eccoptarthroides martynovi | ??????????????0??1 |
| Eccoptarthroides nikitskyi | ??????????????0??1 |
| Pseudobrenthorrhinus magnus | ??????????????0??1 |
| Pseudobrenthorrhinus crassicornis | ??????????????0??1 |
| Brenthorrhinus mirabilis | ??????????????0??1 |
| Gobibrenthorrhinus gigas | ??????????????0??1 |
| Brenthorrhinus brevirostris | ??????????????0??1 |
| Brenthorrhinoides mandibulatus | ????1?????????0??1 |
| Scelocamptus tenuirostris | ??????????????0??1 |
| Brenthorrhinoides robustus | ??????????????0??1 |
| Brenthorrhinoides pubescens | ??????????????0??1 |
| Mongolbrenthorrhinus arnoldii | ??????????????0??1 |
| Mongolbrenthorrhinus pusillus | ??????????????0??1 |
| Mongolbrenthorrhinus flavus | ??????????????0??1 |
| Testudobrenthorrhinus baissiensis | ??????????????0??1 |
| Testudobrenthorrhinus taetricus | ??????????????0??1 |
| Buryatnemonyx niger | ??????????????0??1 |
| Buryatnemonyx tener | ??????????????0??1 |
| Buryatnemonyx gratshevi | ??????????????0??1 |
| Oxycorynoides ponomarenkoi | ??????????????0??1 |
| Procurculio fortipes | ??????????????0??1 |
| Procurculio pallens | ??????????????0??1 |
| Megabrenthorrhinus grandis | ??????????????0??1 |
| Megabrenthorrhinus longicornis | ??????????????0??1 |
| Eccoptarthrus crassipes | ??????????????0??1 |

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|---|---|
| Eccoptothorax latipennis | ??????????????0??1 |
| Distenorrhinus pallidirostris | ??????????????0??1 |
| Distenorrhinus ovatus | ??????????????0??1 |
| Distenorrhinus arnoldii | ??????????????0??1 |
| Distenorrhinus elongatus | ??????????????0??1 |
| Distenorrhinus rotundicollis | ??????????????0??1 |
| Distenorrhinus angulatus | ??????????????0??1 |
| Distenorrhinus major | ??????????????0??1 |
| Distenorrhinus antennatus | ??????????????0??1 |
| Paroxycorynoides elegans | ??????????????0??1 |
| Selengarhynchoides sharyngolensis | ??????????????0??1 |
| Selengarhynchus ovalis | ??????????????0??1 |
| Pseudonemonyx stupendus | ??????????????0??1 |
| Cretonemonyx minimus | ??????????????0??1 |
| Cretonemonyx longirostris | ??????????????0??1 |
| Cretonemonyx profligatus | ??????????????0??1 |
| Megametrioxenoides longus | ??????????????0??1 |
| Megametrioxenoides proelomus | ??????????????0??1 |
| Cretoxenoides erdeniensis | ??????????????0??1 |
| Chinocimberis dispersus | ??????????????0??1 |
| Baissimberis prodigiosus | ??????????????0??1 |
| Mongolocar orcinus (nemonychid) | ??????????????0??1 |
| Karacar contractus (nemonychid) | ??????????????0??1 |
| Baissabrenthorrhinus mirabilis | ??????????????0??1 |
| Ulyaniana nobilis | ????0?????????0??1 |
| Ulyaniana excellens | ????0?????????0??1 |
| Ulyanisca dentipes | ????0?????????0??1 |
| Slonik sibiricus | ????0?????????0??1 |
| Hyperites nadezhkini | |

## 2. Weevils of the Yixian Formation, China (Coleoptera: Curculionoidea): Phylogenetic considerations and comparison with other Mesozoic faunas

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**Abstract**

The weevil fauna of the Yixian Formation, northeastern China, is described and summarized, and its faunal composition compared to other deposits of similar age and older. Thus far it has yielded fossil groups that appear as basal curculionoids, representing a mixture of taxa that belong to extant lineages and possibly extinct stem-groups. It is particularly contrasted to those Mesozoic curculionoids that have been described from the Karatau site of southern Kazakhstan and El Montsec, Spain, the Yixian being quite different from the former due to its younger age. Although diagnoses are provided and characters are discussed, many of the taxonomic categories that are derived from other fossils, and that are referred to here, as well as placements that are made with the material herein, are considered tentative pending a proper cladistic analysis and outline of diagnostic, synapomorphic characters. It is noted that most prior accounts have

suffered from relying on the literature, which is grossly erroneous in many cases, rather than direct examination of fossil type material and this has led to biased interpretations. Taxonomic changes: *Leptocar* Liu and Ren, 2007 = junior synonym of *Cretonanophyes* Zherikhin, 1977; *Cretonanophyes punctatus* Liu and Ren, 2007, resurrected combination; *Cretonanophyes zherikhini* Liu and Ren, 2006, resurrected combination; *Leptocar polychaetus* Liu and Ren, 2007 = junior synonym of *Cretonanophyes zherikhini* Liu and Ren, 2006; *Cretonanophyes rugosithorax* Gratshev and Zherikhin, 2000, resurrected combination; *Montsecanomalus* (*Rugosocar*) Legalov, 2009a = junior synonym of *Cretonanophyes* Zherikhin, 1977; *Chinabrenthorrhinus* Legalov, 2009a = junior synonym of *Chinocimberis* Legalov, 2009b; *Chinocimberis longidigitus* (Ren, 1995), new combination. New species: *Abrocar concavus*, new species; *Abrocar relicinus*, new species.

**Keywords**: Compression fossils, morphology, phylogeny, taxonomy, Cretaceous, Jurassic, Nemonychidae, Eccoptarthridae, Belidae

## Introduction

Weevils (superfamily Curculionoidea) are one of the most diverse groups of extant organisms, with approximately 62,000 described species (Oberprieler *et al.* 2007). They are extremely important economically, being of great agricultural significance because they are associated with all major groups of plants and plant tissues. The current classification of weevils (Curculionoidea), despite having gone through many hypotheses, is still quite unstable at the higher levels and even more so at lower levels (e.g., Franz and Engel 2010). Although there is severe discordance among hypotheses of classification of extant weevils, this incongruence becomes more apparent when extinct groups are considered. Due to the lack of robust morphological character systems, spanning external and internal anatomy, that have been examined and compared across the major weevil clades, placement of fossil taxa has been difficult at best. According to the current understanding of the fossil record, weevils are believed to have diverged from their non-weevil ancestor sometime during the Early to Middle Jurassic, with the oldest definitive weevils found from Late Jurassic deposits. Although some researchers maintain that Obrieniidae Zherikhin and Gratshev (1993) are representative of the earliest described curculionoids from the Late Triassic (Gratshev and Zherikhin 2003; Legalov 2009a, 2010b), most researchers now argue otherwise (Kuschel 2003; Oberprieler *et al.* 2007). Many of the important fossils supporting these findings are from the Late Jurassic Karatau site of southern Kazakhstan, the Early Cretaceous Yixian Formation in northeastern China, and to a lesser extent the Early Cretaceous formations of Crato (Brazil; Aquino Santos de *et al.* 2007; Zherikhin and Gratshev 2004) and El Montsec (Spain; Gratshev and Zherikhin 2000a; Soriano *et al.* 2006; Zherikhin and Gratshev 1997). It should be noted that while many classificatory hypotheses have been proposed and ardently defended including material from the sites mentioned above (particularly from Karatau), little of it (including holotypes) has been re-examined, allowing an abundance of mistakes that are present in the original descriptions and illustrations to be perpetuated. In order to begin to correct these mistakes, material and holotypes pertinent to studying the Yixian weevil fauna have been re-examined, and some of this material is reinterpreted in this paper.

The weevils of the Yixian site are investigated here and represent some of the most primitive groups within the superfamily, such as Nemonychidae Bedel, 1882, and possible representatives of Caridae Thompson, 1992. Although their phylogenetic positions are still under examination, there appears to be a mixture of taxa representing some of the groups as they are defined today, as well as some relict lineages displaying characters suggestive of stem groups. By studying the character systems of important fossils such as those from the aforementioned sites, and incorporating them into phylogenetic analyses that test hypotheses of homology and recognize synapomorphies, the characters defining monophyletic weevil clades can be more confidently outlined and the classification system can reach greater stability.

## Materials and methods

The compression fossils reported herein were recovered from the Yixian Formation of the Jehol Group, northeastern China. The Yixian Formation is dated to approximately the Early Cretaceous by most authors (Late Hauterivian to Early Barremian) (Barrett 2000; Zhou *et al.* 2003; Jiang and Sha 2006), although some controversy remains. Isotopic studies indicate a rough range of ages from 132–112 Ma (Ji *et al.* 2004). Putatively correlative fossils from the Yixian with those in the Solnhofen and Purbeck biotas (although the taxonomic assignments of some taxa in these biota and paraphyletic groups compromise some of these interpretations), along with Yorkshire, Terori-type, and Ryoseki-type floras have led some to consider the formation of Jurassic age (Wang *et al.* 2005). The specimens were studied using a Leica MZ 12.5 stereomicroscope and photographed using an attached Nikon DXM 1200C. To increase visibility and contrast of compressions for photography, a few drops of 95% ethyl alcohol were gently applied to the specimens.

## Results

Systematic Paleontology

Order **Coleoptera** Linnaeus, 1758

Suborder **Polyphaga** Emery, 1886

Infraorder **Cucujiformia** Lameere, 1938

Parvorder **Phytophaga** Dumeril, 1806

Superfamily **Curculionoidea** Latreille, 1802

"Family" **Eccoptarthridae** Arnoldi, 1977

*Comments*. Regarding the lineage that was errected for *Eccoptarthrus crassipes* Arnoldi (1977), namely the Eccoptarthridae, there has been much confusion surrounding its delimitation, as illustrated by the addition of several heterogeneous taxa over the years (Liu and Ren 2006, 2007; Soriano *et al.* 2006). Although this lineage appears to have some affinity to Baissorhynchini Zherikhin (1993) (Baissorhynchina in particular) and Caridae Thompson (1992), such as in the expanded basitarsomeres on the forelegs and similar positions of antennal insertion, these features either appear to be convergent and therefore not a result of shared evolutionary ancestry, or are symplesiomorphies and are features that have been retained from a common ancestor but are not indicative of monophyly. True Eccoptarthridae, more specifically the lineaege defined by *Eccoptarthrus crassipes* Arnoldi (1977) (PIN 2239-1507; Figs 1A, 1B), appear to be found in deposits with a minimum age of Late Jurassic and are particularly defined by their fairly unique rostrum orientation, in which the base of the rostrum is oriented anteriad, forming a right angle (or even acute angle) at the dorsal junction of the rostrum and cranium. Although the holotype of *E. crassipes* is a dorso-ventral compression, it has been observed that in the dorso-ventral compressions of taxa with a rostrum that is linear with respect to the ventral part of the cranium (such as the eobelid group and much of the Karatau material), the entire rostrum is visible, whereby in most other weevil groups that possess a curved rostrum, it is only partially visible in a dorso-ventral compression. It is noted, however, that a very similar condition is observed in several extant nemonychid genera, such as *Acromacer* Kuschel (1989). Moreover, a nearly identical condition has been recently documented in some extant nemonychids, namely *Idiomacer* and *Zimmiellus* Kuschel and Leschen (2011), which is suggestive of a single nemonychid lineage that has persisted since at least the Late Jurassic. Furthermore, the eobelid grouping, as exemplified by *Eobelus longipes* Arnoldi (1977) (PIN 2452-275; Figs 1C, 1D) also appears to share these same characters, suggesting that Eobelidae and Eccoptarthridae are artificial groupings which are actually the same lineage, nested within a more inclusive Nemonychidae (which is indeed the prevailing hypothesis; Kuschel and Leschen 2011). The eobelid head (*Eobelus* sp., PIN 2384-516) also possesses a free labrum (distinct clypeo-labral separation) and distinct sensory setae at the apex of the labrum as in Nemonychidae. In eccoptarthrids, the ventral angle of the junction of the rostrum and cranium is nearly linear, and the gula appears to be present, in which the gular (occipital) sutures are paired and are possibly nearly confluent with the subgenal sulci. A similar condition, interestingly, was diagrammed by Lyal (1995) as representing a hypothetical plesiomorphic curculionoid. The Baissorhynchini, on the other hand, which has been confused with the enigmatic eccoptarthrid group, have a single, medial gular suture, as well as enlarged basitarsomeres on the forelegs (typical of Baissorhynchina) and dense inner apical setal patches on the protibiae. It should be noted that this group (in a comprehensive sense, with the inclusion of the genera *Eccoptarthrus* Arnoldi, 1977 (=*Pseudobrenthorrhinus* Gratshev *et* Zherikhin, 1996), *Procurculio* Arnoldi, 1977, and *Eccoptarthroides* Legalov, 2010) is treated as a subfamily in the family Nemonychidae by

Legalov (2010b). Preliminary evidence from direct examination of Arnoldi's type material certainly supports the notion that Eccoptarthridae (s.str.) and Eobelidae (s.str.) are synonyms, or very closely related, and that both should be subsumed into Nemonychidae should on-going cladistic work continue to corroborate this.

It is also interesting to note that taxa comprising the eccoptarthrid/eobelid lineage or similar in appearance have not been found in the Yixian fauna. Since this lineage is quite abundant in Late Jurassic compressions, it should also be present in the slightly younger, Early Cretaceous (Zhou *et al.* 2003) of Yixian. While this gap may simply be due to a sampling artifact, it may also reflect differences in paleoenvironments.

Family ***Incertae Sedis***

Tribe **Baissorhynchini** Zherikhin, 1993

*Diagnosis*. Compound eyes round to ovoid (or laterally elongated in Abrocarina). Rostrum directed anteriad, slightly curved. Antennae orthocerous, inserted approximately at middle of rostrum or slightly before. Gular (postoccipital) sutures merging medially to form single suture or separate (Abrocarina). Pronotum and elytra with weak, sparse puncturing to fairly dense. Protibiae typically with dense setal patch on inner apical surface or without (Abrocarina); tibiae with two spurs at apex; basitarsomeres expanded (the degree to which may be sexually dimorphic) to slender (Abrocarina).

*Comments*. Although the taxa exhibiting the above character combination appear to form a cohesive group and fall into this described tribe, it is noted that this taxonomic designation, and its two included subtribes, has not been tested phylogenetically and remains ambiguous. This group, in part (namely Baissorhynchina), has a particular affinity to Caridae Thompson, 1992, as defined by Zimmerman (1994), in possessing a dense protibial setal patch on the inner apical surface, similar to the setal brush of many Belidae, expanded probasitarsomeres, and two tibial spurs. The other subtribe, Abrocarina, lack the first two characters and should be included in Nemonychidae (see below). The Baissorhynchina also share with Caridae an elongated antennal scape and single gular (postoccipital) suture; however, the gular sutures do not appear to be entirely confluent (fused) along the ventral surface of the cranium (as in extant Caridae) in some specimens and may only merge at the posterior margin of the cranium near the occipital foramen. Although many of these features are not visible in the holotype of *Baissorhynchus tarsalis* Zherikhin (1977) (PIN 1989-3010; Figs 2A, 2B), they are clear in other undescribed compressions from Baissa (*Baissorhynchus* spp.; PIN 4210-727, Figs 2C, 2D; PIN 3064-7219, Figs 2E, 2F). Although Zherikhin (1977) stated that the labrum in *B. tarsalis* is free, this feature is not visible in the holotype (which is a ventro-lateral compression) nor any other congeners.

Baissorhynchini also has some affinity to Eccoptarthrini Arnoldi, 1977, in possessing expanded probasitarsomeres; however, this character is possibly not a synapomorphy uniting these groups, but rather a parallelism or convergence as suggested by the pattern of other characters. Older deposits from Mongolia, such as those from the Bontsagan Series, and the Karatau site, Kazakhstan, have yielded many more fossils that appear to belong to this group and await inclusion in cladistic analyses to elucidate their positions. The age, abundance, and characterization of this material indicate that small, extant groups, such as Caridae Thompson (1992), perhaps possessed greater historical diversity.

Subtribe **Baissorhynchina** Zherikhin, 1993

*Diagnosis*. Rostrum fairly short to elongate, approximately as long as to more than 2x length of pronotum, broadly curved to nearly straight. Gular (postoccipital) sutures merging medially to form single suture. Eyes round to ovoid. Pronotum and elytra with shallow punctures. Legs often densely covered with setae; forelegs often slightly longer than mid- and hind legs; protibiae with setal brush on inner apical surface; at least probasitarsomeres expanded. Elytra with covering of elongate setae, particularly near apex.

*Comments*. This lineage appears to be the closer of the two subtribes to extant Caridae (*sensu* Zimmerman 1994) and Belidae in terms of synapomorphies and character affinities, in which case the tribe would be paraphyletic and require division. In contrast, the Abrocarina (*vide infra*) are typified by a fairly short rostrum that is more curved and a denser covering of larger punctures on the pronotum and elytra, the Baissorhynchina have a longer rostrum which is straighter and more linear with the ventral surface of the cranium and, in general, a less densely punctured cuticle. Other genera included in this subtribe are *Baissorhynchus* Zherikhin (1977), *Cretocar* Gratshev and Zherikhin (2000), *Emanrhynchus* Zherikhin (1993), *Gobicar* Gratshev and Zherikhin (1999), in part (*G. hispanicus* Gratshev and Zherikhin, 2000), *Gratshevbelus* Soriano (2009), *Hispanocar* Soriano, Gratshev, and Delclòs (2006), *Jarzembowskia* Zherikhin and Gratshev (1997), *Martinsnetoa* Zherikhin and Gratshev (2004), and *Montsecanomalus* Soriano, Gratshev, and Delclòs (2006). *Montsecbelus* Zherikhin and Gratshev (1997) may also belong to this lineage, but closer scrutiny of its characters (as well as the characters of the aforementioned genera included in this subtribe) is direly needed.

Genus ***Cretonanophyes*** Zherikhin

*Cretonanophyes* Zherikhin, 1977: 178 [English edition, 1991: 244]. Type species: *Cretonanophyes longirostris* Zherikhin, 1977. Kuschel (1983: 502); Legalov (2009c: 123) [transfers to Ithyceridae]; Legalov (2010a: 89).

*Leptocar* Liu and Ren, 2007: 642. Type species: *Leptocar polychaetus* Liu and Ren, 2007. Legalov (2009a: 291) [as subgenus in *Montsecanomalus*]; Legalov (2010a: 90). **New synonymy**.

*Montsecanomalus* (*Rugosocar*) Legalov 2009a: 291. Legalov (2010a: 90). **New synonymy**.

*Diagnosis*. Rostrum elongate, slightly more than 2x length of pronotum, nearly straight. Pronotum and elytra with shallow punctures. Legs often densely covered with setae; forelegs often slightly longer than mid- and hind legs. Elytra with covering of elongate setae (not always visible in specimens), particularly near apex.

*Comments*. Due to similar characters in other described genera, such as *Jarzembowskia* Zherikhin and Gratshev (1997), it is probable that other genera should be synonymized aside from *Leptocar*. As has been the case too often in fossil Curculionoidea, many taxa that seem to represent the same species, or are at least congeneric, are often described as different species, genera, and even tribes due to differences in specimen preservation and orientation. The genus *Montsecanomalus* Soriano, Gratshev, and Delclòs (2006), the type species being *M. zherikhini*, also superficially appears similar to *Baissorhynchus*, and whether it possesses a distinct labrum, as reported by the authors, needs to be reassessed.

Legalov (2009c) transferred *Cretonanophyes punctatus* Liu and Ren (2007), *C. zherikhini* Liu and Ren (2007), and *C. rugosithorax* Gratshev and Zherikhin (2000) to *Montsecanomalus* based on the type species of the genus, *C. longirostris* Zherikhin (1977), having slender basitarsomeres on the forelegs and the former three species having inflated basitarsomeres on the forelegs. While the former three species indeed do possess basitarsomeres that are enlarged on the forelegs, *C. longirostris* does as well, as is distinctly visible in the holotype (Figs 3D-3F). However, the illustration given by Zherikhin (1977) is drawn incorrectly, and if referring to this figure one would certainly also come to the conclusion that these taxa are different, which is not the case.

Legalov (2009c) also transferred Baissorhynchini Zherikhin (1993), which includes *Cretonanophyes*, to family Ithyceridae *s. lat.* (sensu Legalov 2009c) based on the lengths of the ventrites, a character which is unfortunately too variable to be of critical importance. While Ithyceridae *s. str.* (the monotypic family including *Ithycerus noveboracensis* (Forster, 1771)) may be related to Attelabidae, there has been no phylogenetic evidence supporting a sister group relationship to Caridae Thompson (1992), and creating such a grouping would be justified only by accepting paraphyletic taxa and grouping based on symplesiomorphies (a method employed by Legalov 2010b). It is fairly certain, though, that *Cretonanophyes* (similar to *Baissorhynchus*) bears strong resemblance to members of extant Caridae (Figs 3G-3J) (Kuschel 1983; Oberprieler *et al.* 2007) based on the inflated basitarsomeres, dense foretibial setal patch, form of the metanotum (particularly the shapes of the metascutum and metascutellum), single (fused) gular suture, and elongated antennal scape. While not all of these features are visible in *C. longirostris* Zherikhin (1977) (PIN 1668-1772, Figs 3D-3F), they are distinct in other undescribed congeners from Karatau (*Cretonanophyes* sp., PIN 4210-7066, Figs 2G, 2H, 3A-3C), as well as those described and reviewed here (Figs 4, 5, 6A-6F). Upon first inspection, members of *Cretonanophyes* and *Baissorhynchus* appear similar to many nemonychids; however, this superficial likeness is immediately dismissed by their possession of a single gular suture and elongated antennal scape. It is possible that *C. longirostris* and *B. tarsalis* may represent male and female of a single species. Given the several species that have been described in both genera, though, as well as those that lay undescribed from Karatau and Baissa, it is unlikely that they are synonymous. Furthermore, the differences in vestiture on the elytra between the two genera appear more significant than a sexual dimorphism.

***Cretonanophyes punctatus*** Liu and Ren, **resurrected combination**

[Figs 4A-5B]

*Cretonanophyes punctatus* Liu and Ren, 2007: 645.

*Montsecanomalus* (*Montsecanomalus*) *punctatus* (Liu and Ren) Legalov (2009a: 291) [in Ithyceridae]; Legalov (2009c: 123); Legalov (2010a: 89).

*Diagnosis*. Rostrum projecting anteriad and fairly straight, only slightly curved. Antennae inserted approximately at middle of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Compound eyes round to ovoid. Pronotum at middle apparently narrower than elytral shoulders. Elytra with fairly sparse covering of elongated setae. Metascutum with concave posterior margin and broadly convex postero-medial margin.

*Description*. Total body length (including rostrum) ca. 5.8 mm. Rostrum slightly longer than 2x length of pronotum. Antennae inserted approximately at middle of rostrum, with weak 3-article club. Compound eyes round to ovoid. Pronotum broadly rounded along lateral margins (no apparent carina) and narrower than anterior of elytra at shoulders. Mesoscutellum triangular.

Metascutum with concave posterior margins and broadly convex postero-medial margins; metascutellum wide. Elytra with faint, shallow striae; dorsal surface covered with sparse, elongate setae; elytra apparently covering tergite 7. Pretarsal ungues (claws) separate.

*Material examined*. CNC-C-LB2006103 (Holotype; Figs 4A, 4B); CNU-C-LB2007105-2 (Figs 4C, 4D), CNU-C-LB2010158, CNC-C-LB2005115 (Figs 4E, 4F), CNU-C-LB2010707 (Figs 4G, 4H), CNU-C-LB2010708 (Figs 5A, 5B).

*Comments*. This combination is resurrected due to its similarity to the type species, *C. longirostris*, in possessing enlarged probasitarsomeres, a rostrum that is at least 2x the length of the pronotum, the presence of elongate, sparse setae on the dorsum, and rostrum of similar length. Although it had been transferred to *Montsecanomalus* Soriano, Gratshev, and Delclòs (2006), there was no explicit basis for this action.

***Cretonanophyes zherikhini*** Liu and Ren, **resurrected combination**

[Figs 5C-6F]

*Cretonanophyes zherikhini* Liu and Ren, 2006: 61.

*Montsecanomalus* (*Montsecanomalus*) *zherichini* (Liu and Ren, 2006). Legalov (2009c: 123); Legalov (2009: 291) [placed in Ithyceridae; *lapsus calami*]; Legalov (2010a: 89) [*lapsus calami*, new combination].

*Leptocar polychaetus* Liu and Ren, 2007: 642. [CNC-C-LB2006101 holotype]. **New synonymy**.

*Montsecanomalus* (*Leptocar*) *polychaetus* (Liu and Ren, 2007); Legalov (2009c: 123); Legalov (2009a: 291); Legalov (2010a: 90) [new combination].

*Diagnosis*. Rostrum projecting anteriad and nearly linear. Antennae inserted slightly before middle of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Compound eyes round to ovoid. Pronotum at middle apparently slightly narrower than elytral shoulders. Procoxae elongate, approximately 0.3x as long as profemora. Elytra with fairly dense covering of elongated setae, particularly near apex. Metascutum with slightly concave posterior margin and broadly convex postero-medial margin.

*Description*. Total body length (including rostrum) ca. 4.1-6.5 mm. Rostrum approximately 2x length of pronotum. Antennae inserted slightly before middle of rostrum, with weak 3-article club. Compound eyes round to ovoid. Pronotum with weak carina along lateral margins and slightly narrower than anterior of elytra at shoulders. Mesoscutellum triangular. Metascutum with slightly concave posterior margins and broadly convex postero-medial margins; metascutellum wide. Elytra with faint, shallow striae; dorsal surface covered with dense, elongate setae, particularly near apex; elytra apparently not covering tergite 7 completely. Pretarsal ungues (claws) separate.

*Material examined*. CNU-C-LB2005103 (original part; Figs 5C, 5D) & CNU-C-LB2005104 (counterpart; Figs 5E, 5F) (Holotype); CNU-C-LB2005109 (Figs 5G, 5H), CNC-C-LB2005113, CNC-C-LB2005112 (Figs 6A, 6B), CNC-C-LB2005114 (Figs 6C, 6D), CNC-C-LB2006101 (Figs 6E, 6F).

*Comments*. This combination is quite similar to *C. punctatus,* but seems to differ largely by the dense, elongate setae on the elytra, the slightly wider pronotum in relation to the elytral shoulders, and more elongated procoxae. Although it had been transferred to *Montsecanomalus* Soriano, Gratshev, and Delclòs (2006), there was no explicit basis for this action; it is therefore resurrected for the same reason as for *C. punctatus* (*vide supra*).

Other included species in the genus *Cretonanophyes* Zherikhin:

***Cretonanophyes longirostris*** Zherikhin [PIN 1668-1772]

[Figs 3D-3F]

*Cretonanophyes longirostris* Zherikhin, 1977: 245. Soriano, Gratshev, and Delclòs (2006: 564); Legalov (2009c: 123) [transfers to Ithyceridae]; Legalov (2010a: 89).

***Cretonanophyes rugosithorax*** Gratshev and Zherikhin, **resurrected combination**

*Cretonanophyes rugosithorax* Gratshev and Zherikhin, 2000: 43. Soriano, Gratshev, and Delclòs (2006: 564).

*Montsecanomalus* (*Montsecanomalus*) *rugosithorax* (Gratshev and Zherikhin, 2000); Legalov (2009c: 123) [new combination].

*Montsecanomalus* (*Rugosocar*) *rugosithorax* (Gratshev and Zherikhin, 2000); Legalov (2009a: 291); Legalov (2010a: 90) [new combination].

*Comments*. This combination is resurrected based on its affinities with *Cretonanophyes longirostris* Zherikhin, including the form and length of the rostrum, enlarged basitarsomeres on the forelegs, and sparse setae on the dorsum. While *C. rugosithorax* appears to be a valid species, its main differences (rugose prothorax) do not justify erection of a monotypic subgenus (*Rugosocar*), particularly given the preservation of these fossils.

### Subtribe **Abrocarina** Legalov, 2009

*Diagnosis*. Rostrum fairly short, slightly more than 1x length of pronotum; gula apparently present , narrow (gular [postoccipital] sutures paired); shallow scrobe present along basal half of rostrum. Compound eyes laterally elongated. Pronotum with acute lateral margin, narrower than anterior of elytra at shoulders. Pronotum and elytra with fairly dense covering of punctures. Body with short, sparse setae. First probasitarsomere not to slightly expanded.

*Comments*. While the Abrocarina appear to form a cohesive group, its inclusion in Baissorhynchini is doubtful. In possessing an apparent gula, absence of protibial brushes, and probasitarsomeres that typically are quite slender, the Abrocarina more likely should be transferred to Nemonychidae and seem to represent an early lineage within the family as suggested by similar specimens with extant and extinct genera, such as *Cratomacer* Zherikhin and Gratshev (2004). Whether this group is inclusive in Baissorhynchini and sister to Baissorhynchina, as well as the above hypotheses, have yet to be tested in a cladistic framework.

### Genus ***Abrocar*** Liu and Ren

*Abrocar* Liu and Ren, 2006: 62. Type species: *Abrocar brachyorhinos* Liu and Ren, 2006.

Legalov (2009c: 121) [placed in Ithyceridae]; Legalov (2009a: 291); Legalov (2010a: 88).

*Diagnosis*. As for the subtribe (*vide supra*).

*Comments*. As is the case with *Cretonanophyes*, there appears to be a few described genera that fall into the definition of *Abrocar*, such as *Gobicar* Gratshev and Zherikhin (1999), in part (*G. ponomarenkoi*). As for the placement of *Abrocar* in Eccoptarthrini (Ithyceridae) by Legalov (2009c), there are no apparent features that would justify such a relationship. For example, Eccoptarthrini (as illustrated by *Eccoptarthrus crassipes* and related species) is somewhat diagnosed by the orientation of the rostrum, in which it projects anteriad from the cranium and from the ventral surface, a feature not exhibited by species of *Abrocar*. Other characters possessed by many Eccoptarthini, and not by *Abrocar*, include inflated femora and expanded basitarsomeres.

***Abrocar brachyorhinos*** Liu and Ren

[Figs 6G-8D]

*Abrocar brachyorhinos* Liu and Ren, 2006: 64. Legalov (2009: 291); Legalov (2010a: 89).

*Diagnosis*. Rostrum projecting anteriad, broadly curved; weak scrobe along basal half of rostrum, ending just before compound eye. Antennae inserted approximately at middle of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Pronotum at middle slightly narrower than elytral shoulders; lateral margin with weak carina; dorsal surface with fairly dense punctures. Pronotum and elytra apparently with sparse setae. Elytra with fairly dense covering of large punctures along elytral striae and intervals; elytra moderately convex. Probasitarsomere apparently not expanded.

*Description*. Total body length (including rostrum) ca. 3.4-4.0 mm. Rostrum slightly longer than pronotum to 1.5x length of pronotum. Antennae inserted approximately at middle of rostrum, with weak 3-article club. Compound eyes laterally elongated. Pronotum with weak carina along lateral margins and slightly narrower than anterior of elytra at shoulders. Elytra with rather deep striae, striae and intervals with dense punctures; elytra fairly convex, apparently covering tergite 7 completely. Pretarsal ungues (claws) separate, diverging.

*Material examined*. CNU-C-LB2005105 (Holotype; Figs 6G, 6H); CNU-C-LB2005125 (Figs 7A, 7B), CNU-C-LB2005119 (Figs 7C, 7D), CNU-C-LB2010701 (original part; Figs 7E, 7F) & CNU-C-LB2010703 (counterpart; Figs 7G, 7H), CNU-C-LB2010705 (original part; Figs 8A, 8B) & CNU-C-LB2010706 (counterpart; Figs 8C, 8D).

***Abrocar macilentus*** Liu and Ren

[Figs 8E-9F]

*Abrocar macilentus* Liu and Ren, 2007: 644. Legalov (2009: 291); Legalov (2010a: 89).

*Diagnosis*. Rostrum projecting anteriad, broadly curved; weak scrobe along basal half of rostrum, ending just before compound eye. Antennae inserted approximately at middle of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Pronotum at middle slightly narrower than elytral shoulders; lateral margin with weak carina; dorsal surface with fairly dense punctures. Pronotum and elytra apparently with sparse setae. Elytra with fairly large, dense covering of punctures along elytral striae and intervals; elytra weakly convex, slightly compressed dorso-ventrally. Probasitarsomere apparently not expanded.

*Description*. Total body length (including rostrum) ca. 3.2-3.4 mm; body slightly compressed dorso-ventrally. Rostrum slightly longer than pronotum to 1.5x length of pronotum. Antennae inserted approximately at middle of rostrum, with weak 3-article club. Pronotum with weak carina along lateral margins and slightly narrower than anterior of elytra at shoulders. Elytra with rather deep striae, striae and intervals with dense punctures; elytra broadly convex, apparently covering tergite 7 completely. Pretarsal ungues (claws) separate, diverging.

*Material examined*. CNU-C-LB2006102 (Holotype; Figs 8E, 8F); CNU-C-LB2005110 (Figs 8G, 8H), CNU-C-LB2010151, CNU-C-LB2007103 (Figs 9A, 9B), CNU-C-LB2010157, CNU-C-LB2010156 (Figs 9C, 9D), CNU-C-LB2010704 (Figs 9E, 9F).

*Comments*. While Liu and Ren (2007) provide a few features to distinguish *A. macilentus* from *A. brachyorhinos*, those features are found not to be diagnostic and are present in both species. While the species initially appear conspecific and have many characters in common, the most striking feature of *A. macilentus* is its more dorso-ventrally compressed body and apparently more slender and longer legs. These features seem to effectively separate the fossils into the two species described above; however, with the study of more material (such as from deposits in Mongolia, Kazakhstan, and Siberia), it is possible that these features could be regarded as intraspecific variation.

## ***Abrocar concavus*, new species**

[Figs 9G-10B]

*Diagnosis*. Rostrum projecting anteriad, broadly curved; scrobe apparently absent or only slight. Pronotum with medial impression, acute lateral margins; dorsal surface with fairly dense, shallow punctures. Pronotum and elytra apparently with sparse setae. Elytra with fairly dense covering of punctures along elytral striae and intervals; elytra weakly convex, compressed dorso-ventrally. Probasitarsomere apparently slightly expanded.

*Description*. Total body length (including rostrum) ca. 4.3 mm; body compressed dorso-ventrally. Rostrum slightly longer than length of pronotum. Antennae not visible. Pronotum with medial impression; acute lateral margins. Elytra with rather shallow striae, striae and intervals with dense, shallow punctures; elytra broadly convex, apparently covering tergite 7 completely. Femora slightly swollen. Pretarsal ungues (claws) not visible.

*Material examined*. CNU-C-LB2007105 (original part [Figs 9G, 9H] & counterpart [Figs 10A, 10B]) (Holotype).

*Etymology*. The specific epithet "*concavus*" is Latin for concave or arched inward, referring to the impression on the pronotum.

*Comments*. This species appears quite different from *A. macilentus* and *A. brachyorhinos* by the more dorso-ventrally compressed body form and the medial impression on the pronotum.

## ***Abrocar relicinus*, new species**

[Figs 10C-10H]

*Diagnosis*. Body moderately punctured. Rostrum projecting antero-ventrally, moderately curved; scrobe apparently along basal half of rostrum and shallow. Pronotum only slightly narrower than anterior of elytra at shoulders to approximately equal in width; pronotum with weakly acute lateral margins.

*Description*. Total body length (including rostrum) ca. 2.5-2.6 mm. Rostrum slightly longer than length of pronotum to 1.5x as long, slightly widening apically; mandibles visible, fairly large. Antennae inserted just before middle of rostrum. Eyes laterally elongated. Pronotum with weakly acute lateral margins. Mesonotum apparently with transverse ridges, possibly a stridulatory file. Pronotum and elytra with striae, striae and intervals with moderately dense punctures; elytra broadly convex. Probasitarsomere not enlarged or only slightly expanded. Pretarsal ungues (claws) separate, diverging.

*Material examined*. CNU-C-LB2010152 (Holotype; Figs 10C, 10D). CNU-C-LB2005116 (original part and counterpart; Figs 10E, 10F), CNU-C-LB2005117, CNU-C-LB2005118, CNU-C-LB2010160, CNU-C-LB2005122 (Figs 10G, 10H).

*Etymology*. The specific epithet "*relicinus*" is Latin for bent backward, referring to the more curved form of the rostrum of this species as compared to its congeners.

*Comments*. This species appears fairly similar to its congeners having a moderately punctured cuticle, but differs particularly in the form of its rostrum, in which it is oriented antero-ventrally. Other species in *Abrocar* appear to have a rostrum that is oriented more anteriad, in which the ventral angle where the rostrum meets the cranium is greater. The possible presence of a stridulatory file (Figs 10G, 10H) could indicate a relationship within Nemonychidae or close to it, particularly since extant Rhinorhynchinae possess a stridulatory file in this region.

**Gen. sp.? indeterminate 1**

[Figs 11A, 11B]

*Diagnosis*. Rostrum projecting anteriad, broadly curved, slightly widening apically; scrobe apparently along basal half of rostrum and shallow. Compound eyes slightly laterally elongated. Pronotum narrower than anterior of elytra at shoulders; pronotum with weakly acute lateral margins.

*Description*. Total body length (including rostrum) ca. 3.0 mm. Rostrum slightly longer than length of pronotum, gradually widening apically; mandibles visible, fairly large. Antennae inserted approximately along middle of rostrum. Pronotum with weakly acute lateral margins. Pronotum and elytra with striae, striae and intervals with moderately dense punctures; elytra broadly convex. Pretarsal ungues (claws) not visible.

*Material examined*. CNU-C-LB2010154.

*Comments*. Although this specimen roughly appears similar to *A. macilentus* and *A. brachyorhinos* in body form, many of its features are preserved too poorly to properly identify it. It is not identified here as either of the former two species due to the slight widening of the rostrum apically, a feature not observed in these other species. The position of the rostrum on the head, in which it is oriented anteriad and the junction between the rostrum and cranium nearly forming a right angle dorsally, is a feature similar to eobelids, as well as some extant nemonychids. In fact, the resemblance of this specimen to *Acromacer* Kuschel (1989) is quite strong (considering the few visible features in the fossil), such as the orientation of the rostrum and its gradual widening apically. By describing it here, if other material is found that can be attributed to this specimen then a more objective decision can be made as to its identification.

Family **Nemonychidae** Bedel, 1882

Subfamily **Brenthorrhininae** Arnoldi, 1977

Tribe ***Incertae Sedis***

Genus ***Brenthorrhinoides*** Gratshev and Zherikhin, 1996

*Brenthorrhinoides* Gratshev and Zherikhin, 1996: 119. Type species *Brenthorrhinoides mandibulatus* Gratshev and Zherikhin, 1996. Legalov (2009a: 289); Legalov (2009c: 121) [transfer to Ithyceridae]; Legalov (2010a: 83) [transfer to Nemonychidae].

*Diagnosis*. Rostrum projecting anteriad from ventral surface of the cranium, fairly straight, only slightly curved; gula present (gular sutures paired). Antennae inserted slightly beyond middle of rostrum to near apex; antennal club weak, club articles barely larger than flagellar articles. Compound eyes slightly elongated, ovoid. Pronotum with acute lateral margin; pronotum narrower than elytral shoulders. Pronotum and elytra moderately punctured, with short, sparse setae. Elytra with distinct, punctured striae.

*Comments*. Although the three nemonychid taxa described from Yixian were originally placed in *Brenthorrhinoides*, following examination of the type species (PIN 2239-1508; Figs 11B, 11C), the genus evidently belongs in the eobelid grouping (Legalov 2009a, 2010a), due mostly to its ventral rostrum orientation. It is difficult to provide a diagnosis for this genus (and others represented in Karatau) due to many similar genera (which are often also placed in different tribes and subfamilies!). Its monophyly, therefore, is questionable. Although *Brenthorrhinoides* was placed in the tribe Brenthorrhinoidini by Legalov (2003), the tribe then subsequently placed in Rhynchitidae (Legalov 2005), the characters in support of these placements are not synapomorphic (and given that maxillae are almost never visible in compression fossils, the use of a maxillary character is likely not informative) and do not warrant erection of a new tribe nor placement in Rhynchitidae. Thus, this placement seems dubious pending a proper cladistic treatment and statement of supporting characters. Their inclusion in Brenthorrhininae seems to support a fairly cohesive grouping, as does their placement in the eobelid grouping (Alonso-Zarazaga and Lyal 1999), producing a grouping of taxa with rather linear rostra which protrude from the ventral surface of the cranium. The taxonomic rank of Eobelidae is somewhat uncertain, however, and whether it constitutes a separate sister-group clade, stem-group lineage, or more likely one group nested within Nemonychidae, the latter being the current favored hypothesis (Gratshev and Zherikhin 1996; Kuschel 1983, 2003; Kuschel and Leschen 2011; Legalov 2010b), requires more rigorous cladistic treatment. As *Brenthorrhinoides* is of the eobelid group, like the other eobelids, it has not been found in Yixian.

Subfamily **Cimberidinae** Gozis, 1882

Tribe **Cimberidini** Gozis, 1882

Genus ***Chinocimberis*** Legalov, 2009b

*Chinocimberis* Legalov, 2009b: 205. Type species: *Brenthorrhinoides angustipecteris* Liu, Ren, and Tan, 2006. Legalov (2010a: 86).

*Chinabrenthorrhinus* Legalov, 2009a: 290. Type species: *Brenthorrhinus longidigitus* Ren, 1995. Legalov, 2009a: 290; Legalov (2010a: 84). **New synonymy**.

*Diagnosis*. Body moderately compressed dorso-ventrally. Rostrum projecting anteriad and fairly straight, only slightly curved; labrum small. Antennae inserted near apex of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Head angular before base of rostrum. Compound eyes slightly elongate, ovoid, bulging. Pronotum with acute lateral margin; lateral margins nearly parallel, posterior of pronotum only slightly wider than anterior. Pronotum and elytra with dense covering of elongate setae. Elytra with small punctures, if any, sparsely arranged (not in striae).

*Comments*. The genus *Chinabrenthorrhinus* Legalov (2009a), which was created to accommodate *Brenthorrhinus longidigitus* Ren (1995), is synonymized here with *Chinocimberis* Legalov (2009b) based mainly on the form of its rostrum, which does not appear to originate from the ventral surface of the cranium as it does in Brenthorrhininae. The placement of *Chinocimberis* in Cimberidinae is mainly supported by the absence of distinct punctate striae on the elytra; on the other hand, it is considered tentative and temporary, particularly given the differences in nemonychid classification between Kuschel (1983, 1994) and Alongso-Zarazaga and Lyal (1999).

***Chinocimberis angustipecteris*** (Liu, Ren, and Tan)

[Figs 11E-12B]

*Brenthorrhinoides angustipecteris* Liu, Ren, and Tan, 2006: 608.

*Chinocimberis angustipecteris* Legalov, 2009b: 205 [new combination]. Legalov (2010a: 86).

*Diagnosis*. Body moderately compressed dorso-ventrally. Rostrum projecting anteriad and fairly straight, only slightly curved. Antennae inserted near apex of rostrum; antennal club weak, club articles barely larger than flagellar articles. Head angular before base of rostrum. Compound eyes slightly elongate, ovoid. Pronotum with acute lateral margins; lateral margins nearly parallel, posterior of pronotum only slightly wider than anterior. Pronotum and elytra with dense covering of elongate setae.

*Description*. Total body length (including rostrum) ca. 6.2-6.5 mm. Rostrum approximately equal in length to pronotum. Antennae with slight club, inserted near apex of rostrum. Eyes ovoid. Pronotum with distinctly acute lateral margins; slightly narrower than elytral shoulders. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight, flattened; striae not visible; elytra apparently not covering tergite 7 completely or barely covering it. Mesoscutellum triangular. Metanotum with postero-medial margin strongly concave and metascutellum forming two lateral, ovoid lobes. Tarsae not clearly visible.

*Material examined*. CNU-C-LB2005102 (Holotype; Figs 11E, 11F); CNU-C-LB2005127 (Figs 11G, 11H), CNU-C-LB2007104 (Figs 12A, 12B).

*Comments*. While Legalov (2009b) transferred *Brenthorrhinoides angustipecteris* and *B. magnoculi* to the new genus *Chinocimberis*, this move was made with little justification and is difficult to accept, particularly since a very similar species, *B. latipecteris* Liu, Ren, and Tan (2006) was transferred to the monotypic genus, *Renicimberis* Legalov (2009b), also with little justification. However, beyond any subtle differences in pronotal width or antennal insertion, there seems to be a fundamental difference between *Chinocimberis* and *Brenthorrhinoides* that also reflects their placement in different subfamilies, namely the orientation of the rostrum. In *Brenthorrhinoides* (Brenthorrhininae), the rostrum is oriented ventrally with the ventral surface of the cranium and directed nearly straight anteriad, whereas in *Chinocimberis* the rostrum in oriented more medially on the cranium. As mentioned above, though, until a more strict analysis has been conducted including these groups in a larger framework of taxa and characters, the proposed relationships should be regarded as preliminary.

***Chinocimberis magnoculi*** (Liu, Ren, and Tan)

[Figs 12C-13B]

*Brenthorrhinoides magnoculi* Liu, Ren, and Tan, 2006: 608.

*Chinocimberis magnoculi* Legalov, 2009b: 205. Legalov (2010a: 87).

*Diagnosis*. Body moderately compressed dorso-ventrally. Rostrum projecting anteriad and fairly straight, only slightly curved. Antennae inserted near apex of rostrum; antennal club weak, club articles barely larger than flagellar articles. Head angular before base of rostrum. Compound eyes slightly elongate, ovoid. Pronotum with acute lateral margins; trapezoidal, anterior of pronotum narrower than posterior. Pronotum and elytra with moderately dense covering of elongate setae. Elytra with small, sparse punctures not arranged in striae.

*Description*. Total body length (including rostrum) ca. 5.3-5.4 mm. Rostrum approximately equal in length to pronotum; occipital and subgenal sulci apparently separate. Mandibles large. Antennae with slight club, inserted near apex of rostrum. Compound eyes ovoid. Pronotum with distinctly acute lateral margins; slightly narrower than elytral shoulders. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight, flattened; faint, shallow striae visible; elytra covering tergite 7 completely. Metathorax not visible. Tarsae not clearly visible.

*Material examined*. CNU-C-LB2005107 (original part; Figs 12C, 12D) & CNU-C-LB2005108 (counterpart; Figs 12E, 12F) (Holotype). CNU-C-LB2010155 (Figs 12G, 12H), CNU-C-LB2010702 (Figs 13A, 13B).

*Comments*. As both *Chinocimberis angustipecteris* and *C. magnoculi* possess fairly short rostra (approximately equal in length to the pronota), the main distinguishing feature between them appears to be the wider body of *C. magnoculi* and its more trapezoidal pronotum.

Other included species in the genus *Chinocimberis* Legalov:

***Chinocimberis longidigitus*** (Ren), **new combination**

*Brenthorrhinus longidigitus* Ren, 1995: 90. Soriano, Gratshev, and Delclòs (2006) [*Brenthorrhinus longidigitatus*, *lapsus calami*]; Legalov (2009b: 210) [*Brenthorrhinus longidigitatus*, *lapsus calami*].

*Chinabrenthorrhinus longidigitatus* (Ren); Legalov, 2009a: 290 [*lapsus calami*, new combination]; Legalov (2010a: 84) [*lapsus calami*].

*Diagnosis*. Body moderately compressed dorso-ventrally. Rostrum projecting anteriad and fairly straight, only slightly curved, widening apically. Antennae inserted near apex of rostrum; antennal club weak, club articles slightly larger than flagellar articles. Head angular before base of rostrum. Compound eyes slightly elongate, ovoid. Pronotum with acute lateral margins; lateral margins nearly parallel, posterior of pronotum only slightly wider than anterior. Pronotum and elytra with moderately dense covering of elongate setae.

*Comments*. Given the similar profile of this species to *Chinocimberis angustipecteris* (Liu, Ren, and Tan), it is likely to be synonymous with that taxon.

Genus ***Renicimberis*** Legalov, 2009b

*Renicimberis* Legalov, 2009b: 206. Type species: *Brenthorrhinoides latipecteris* Liu, Ren, and Tan, 2006. Legalov (2009a: 290); Legalov (2010a: 87).

*Diagnosis*. Body moderately compressed dorso-ventrally. Rostrum projecting anteriad and fairly straight, only slightly curved; rostrum slightly longer than to nearly 1.5x length of pronotum Antennae inserted near apex of rostrum; antennal club weak, club articles barely larger than flagellar articles. Head angular before base of rostrum. Compound eyes slightly elongate, ovoid. Pronotum with acute lateral margins; slightly narrow than elytral shoulders; pronotum widest at middle. Pronotum and elytra with moderately dense covering of elongate setae. Elytra lacking punctures.

*Comments*. The genus *Renicimberis* Legalov (2009b) was created to accommodate *Brenthorrhinoides latipecteris* Liu, Ren, and Tan (2006) based on the width of the pronotum and the presence of weak elytral striae. Although members of *Chinocimberis* also share some of these character states, the pronotum of *Renicimberis* is widest approximately at the middle, whereas in *Chinocimberis* it is widest at the posterior angle, and the rostrum of *Renicimberis* also is longer. While small punctures appear to be present in some members of these two genera, they do not form distinct striae as indicated by Liu *et al.* (2006). It is possible that such superficial features are sexual dimorphisms, but for now the differences at least appear to be distinguishable and consistent. Also, similar to the others nemonychids discussed above, many of the fossils are preserved well enough to show that their metanota were very similar to those of extant specimens (Fig. 13C).

***Renicimberis latipecteris*** (Liu, Ren, and Tan)

[Figs 13D-14B]

*Brenthorrhinoides latipecteris* Liu, Ren, and Tan, 2006: 608.

*Renicimberis latipeeteris* Legalov, 2009b: 206 [*lapsus calami*, new combination]; Legalov (2009a: 290); Legalov (2010a: 87).

*Diagnosis*. As for the genus (*vide supra*).

*Description*. Total body length (including rostrum) ca. 6.3-7.5 mm. Rostrum slightly longer than to nearly 1.5x length of pronotum; occipital and subgenal sulci apparently separate, subgenal sulci apparently separate along full length of rostrum; mandibles large. Antennae with slight club, inserted near apex of rostrum. Compound eyes ovoid. Pronotum with distinctly acute lateral margins; slightly narrower than elytral shoulders. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight, flattened; small, faint, punctures visible; striae apparently absent; elytra covering tergite 7 completely. Mesoscutellum apparentely semicircular. Metanotum with postero-medial margin strongly concave and metascutellum forming two lateral, ovoid lobes. Tarsae not clearly visible.

*Material examined*. CNU-C-LB2005101 (Holotype; Figs 13D, 13E). CNU-C-LB2007101 (Figs 13F, 13G), CNU-C-LB2005123 (Figs 13H, 13I), CNU-C-LB2010153 (Figs 14A, 14B).

*Comments*. *Renicimberis* is monotypic. As mentioned above, it is distinguishable from *Chinocimberis* based mainly on the pronotum being widest approximately at the middle and the longer rostrum, slightly less than 1.5x the length of the pronotum.

### Family **Belidae**? Schönherr, 1826

Genus ***Microprobelus***? Liu, Ren, and Shih, 2006

***Microprobelus liuae*** Liu, Ren, and Shih

[Figs 14C-14F]

*Microprobelus liuae* Liu, Ren, and Shih, 2006: 886. [placed in Belidae: Eobelinae]. Legalov (2009b: 204) [placed in Nemonychidae: Eobelinae]; Legalov (2010a: 77).

*Diagnosis*. Rostrum projecting antero-ventrally and fairly straight, only slightly curved. Antennae inserted slightly beyond middle of rostrum; antennal club weak, club articles barely larger than flagellar articles. Compound eyes round. Pronotum with acute lateral margin, extending dorsally towards posterior margin. Pronotum and elytra with dense covering of elongate setae. Tibiae with longitudinal, crenulated carina along outer margin. Tarsomeres slightly lobed.

*Description*. Total body length (including rostrum) ca. 7.2-9.0 mm. Rostrum approximately 1.5x length of pronotum. Antennae with slight club, inserted just beyond middle of rostrum. Compound eyes round. Pronotum with acute lateral margin extending dorsally along posterior margin. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight along disc, gradually curving apically; elytra with faint striae, apparently not covering tergite 7. Tibiae with two small apical spurs. Tarsomeres slender and slightly lobed. Pretarsal ungues (claws) separate, diverging, and with small inner tooth on each claw.

*Material examined*. CNU-C-LB2005106 (Holotype; Figs 14C, 14D). CNU-C-LB2007102 (Figs 14E, 14F).

*Comments*. This species does appear to share many affinities with Belidae, such as the protibial setal brush along the inner apical surface (Figs 14C, 14D, 15B), a longitudinal, crenulated carina along the outer margin of the tibiae (similar to modern belids; Figs 15D, 15E), and the lobed tarsomeres (Fig. 15C). Although the holotype at least also appears to have a similar metanotum to extant belids (Fig. 15A), aside from its general belid gestalt and the homoplasious features mentioned by Liu *et al.* (2006), it is difficult to identify any other informative characters that would place it in this family. While it is likely that this species is more closely related to Belidae or its sister groups, and these features certainly suggest a closer relationship to Belidae than *Davidibelus* Zherikhin and Gratshev (2004) to Belidae, for example, another possibility could include a position closer to Nemonychidae due to its toothed pre-tarsal claws, or to Anthribidae due to the nature of the lateral margin of the pronotum in this species; however, a more informed placement should await its inclusion in a phylogenetic analysis.

Family ***Incertae Sedis***

**Gen. sp. indeterminate 2**

[Figs 15F, 15G]

*Diagnosis*. Rostrum projecting anteriad and fairly straight, only slightly curved. Antennae inserted near apex of rostrum; antennal club weak, club articles barely larger than flagellar articles. Compound eyes round. Pronotum with acute lateral margin, extending dorsally towards posterior margin. Pronotum and elytra with fairly dense covering of elongate setae. Metascutum strongly concave along postero-medial margin.

*Description*. Total body length (including rostrum) 5.1 mm. Rostrum approximately equal in length to pronotum. Antennae with slight club, inserted near apex of rostrum. Compound eyes small, round. Pronotum with acute lateral margin extending dorsally along posterior margin. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight and broadly curved; elytra with faint striae, apparently covering tergite 7. Metascutum with strongly concave posterior margin and acute postero-medial margin (the metascutellum thus forming two ovoid shapes laterally). Pretarsal ungues (claws) not visible.

*Material examined*. CNU-C-LB2005111.

*Comments*. This specimen bears some resemblance to *M. liuae* in the acute lateral margin of the pronotum, but other features seem to substantially differentiate them. For example, the rostrum of this specimen is directed more anteriad and it possesses antennae that are inserted near the apex of the rostrum. Although it is difficult to interpret in the fossil, as it seems the pterothorax is slightly separated from the prothorax, it also appears to have a metascutum that is strongly concave along the postero-medial margin, a form which is typical of extant Nemonychidae. If indeed a nemonychid, as it lacks any distinct elytral striae, it could be placed in Cimberidinae.

**Gen. sp. indeterminate 3**

[Figs 15H, 15I]

*Diagnosis*. Rostrum projecting antero-ventrally and fairly straight, slightly curved. Antennae inserted near apex of rostrum; antennal club weak, club articles barely larger than flagellar articles. Compound eyes slightly ovoid. Pronotum with acute lateral margin. Pronotum and elytra with fairly dense covering of elongate setae. Femora inflated.

*Description*. Total body length (including rostrum) 5.4 mm. Rostrum slightly longer than length of pronotum. Antennae with weak club, inserted near apex of rostrum. Compound eyes small, slightly ovoid. Pronotum with acute lateral margin, apparently extending dorsally along posterior margin. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight and broadly curved; striae not visible; elytra apparently covering tergite 7. Femora inflated, particularly metafemora. Tarsomeres shallowly lobed. Pretarsal ungues (claws) separate, diverging.

*Material examined*. CNU-C-LB2010159.

*Comments*. This specimen also bears some resemblance to *M. liuae*, as well as gen. sp. indeterminate 1, the former in the lobed tarsomeres, the latter in the apical antennal insertion on the rostrum, and both in the form of the acute lateral margin of the pronotum and the dense covering of setae on the pronotum and elytra. This specimen differs, however, particularly in the inflated femora. It is possible that this specimen is conspecific with gen. sp. indeterminate 1, in which the inflated femora are a sexual dimorphism, and may be closer to Nemonychidae. Also as mentioned above, it could be placed in the nemonychid subfamily Cimberidinae due its lack of elytral striae.

Family **Nemonychidae**? Bedel, 1882

**Gen. sp. indeterminate 4**

[Figs 16A-16F]

*Diagnosis*. Rostrum slender, projecting antero-ventrally and fairly straight, broadly curved. Antennae inserted slightly beyond middle of rostrum; antennal club weak. Compound eyes slightly ovoid. Pronotum with acute lateral margins extending dorsally. Pronotum and elytra with fairly dense covering of elongate setae.

*Description*. Total body length (including rostrum) ca. 6.0 mm. Rostrum slightly longer than length of pronotum. Antennae with weak club, inserted beyond middle of rostrum near apex. Compound eyes small, ovoid. Pronotum with distinctly acute lateral margins, extending dorsally along posterior margin. Pronotum and elytra densely covered with elongate setae. Elytra fairly straight and broadly curved; striae not visible; elytra apparently covering tergite 7. Femora fairly slender. Tarsomeres not clearly visible. Pretarsal ungues (claws) not visible.

*Material examined*. CNU-C-LB2007104-2 (original part [Figs 16A, 16B] and counterpart [Figs 16C, 16D]), CNU-C-LB2010709 (Figs 16E, 16F).

*Comments*. This species, similar to the previous two indeterminate species, possesses antennae that are inserted closer to the apex of the rostrum, rather strongly acute lateral margins of the pronotum that extend dorsally along the posterior margin of the pronotum, and a dense covering of setae on the pronotum and elytra. This species probably is more closely related to Nemonychidae given its general appearance, and most likely could be classified in Cimberidinae or near it due to the lack of elytral striae; however, superficial features such as these are not very reliable in placing fossils in a higher classification and should await the inclusion of specimens that exhibit more informative features.

Family **Anthribidae**? Billberg, 1820

**Gen. sp. indeterminate 5**

[Figs 16G, 16H]

*Diagnosis*. Rostrum projecting anteriad, broadly curved; weak scrobe along basal half of rostrum, ending just before eye. Antennae inserted approximately at middle of rostrum; antennal club weak, club articles distinctly larger than flagellar articles. Compound eyes laterally elongate. Pronotum narrow at middle and widening posteriorly; lateral margins with strong carinae; posterior margin with prebasal transverse carina. Abdominal tergite 7 elongate and curved ventrally.

*Description*. Total body length (including rostrum) 2.0 mm. Rostrum approximately equal in length to pronotum. Antennae inserted approximately at middle of rostrum, with weak 3-article club. Compound eyes laterally elongate. Pronotum widening posteriorly, with strong carina along lateral margins, particularly along posterior half; posterior margin apparently with strong prebasal transverse carina with numerous small ridges or blunt teeth. Pronotum and elytra with dense, shallow punctures. Elytra rounded apically, not covering tergite 7 completely, ending along anterior margin of tergite; tergite 7 enlarged and extending ventrally. Ventrites short, subequal in length, and strongly round. Legs slender; tarsomere 3 short. Pretarsal ungues (claws) separate, diverging.

*Material examined*. CNU-C-LB2005126.

*Comments*. This specimen at first appears to belong in Abrocarina, or at least Nemonychidae, given the fairly short antennae and the similar gestalt of these groups; however, upon closer inspection the elongate seventh tergite protruding from underneath the elytra, similar to modern anthribids (Fig. 16I), is immediately noticeable, although a median groove is not visible in this compression. The apparent presence of a prebasal transverse carina on the pronotum and strong lateral carinae, other features characteristic of extant anthribids (Fig. 16J), also lend evidence that this specimen likely is a rather long-snouted anthribid and not a nemonychid. The structure of the ventrites are also quite anthribid-like, short and appearing strongly curved. The fossil record of Anthribidae in the Mesozoic is indeed quite sparse and rather dubious, consisting of *Cretanthribus* Legalov (2009a), *Anthribidites* Zherikhin (1993), and *Chretochoragus* Soriano, Gratshev, and Delclòs (2006).

**Discussion**

*The Yixian weevil composition* (Table 1):

From investigations of the specimens uncovered to date and examination of the visible character systems in the fossils, weevils of the Yixian appear to represent the past diversity of both extant and extinct groups. The composition of this site, in contrast to that of Karatau, does not appear to contain specimens of the extinct forms in Eobelidae (*sensu* Arnoldi 1977) possessing rostra emerging from the ventral surface of the head (e.g. Eobelini Arnoldi 1977 and Procurculionini Arnoldi 1977) or Ulyanidae Zherikhin, 1993 (Gratshev 1998). The groups appearing close to the majority of Nemonychidae are those of *Chinocimberis* Legalov (2009b) and *Renicimberis* Legalov (2009b) (Cimberidinae [those formerly described in *Brenthorrhinoides* and *Brenthorrhinus*]). These groups often have dense, stiff setae on the pronotum and elytra, a rostrum that abruptly widens apically, and when visible, a metanotum that possesses a metascutum with acute postero-medial margins and strongly convex posterior margins, typical of modern Nemonychidae (Figs 13C).

In some Baissorhynchini, constituting much of the other taxa from Yixian, it is also possible to see outlines of the metascutum, in which the postero-medial margins are more angular or rounded and the posterior margins are strongly convex, similar to modern Caridae (*sensu* Zimmerman 1994; Fig. 3J) and many Belidae (Fig. 15A). The Baissorhynchina also possess enlarged probasitarsomeres and inner apical, dense setal patches on the protibiae, resembling Caridae (Fig. 3H) and Belidae (Fig. 15B).

It will be quite interesting if taxa representing the eobelid/eccoptarthrid lineage are found in older fossil biotas in China, such as Daohugou or Jiulongshan, which are dated to approximately Late Jurassic or slightly older (Gao and Ren 2006; Rasnitsyn and Zhang 2004; Wang *et al.* 2005). A finding such as this would provide more robust evidence that diverse weevil groups which flourished on gymnosperms during the Jurassic, such as the eccoptarthrid/eobelid lineage, decreased in abundance and became part of a faunal turnover during the Early Cretaceous as angiosperms began to dominate the landscape (Oberprieler *et al.* 2007).

*Defining higher-level taxa:*

At the start we must reiterate that we are using the higher classification of Mesozoic curculionoids as it presently stands but note that groups like Eobelidae and Eccoptarthridae will likely be subsumed under other lineages once cladistic work is completed (Davis in prep.), as also hypothesized by several authors (see below). Thus, our position for the moment is a strictly conservative one reserving the more formal changes until the phylogeny is more explicitly elucidated.

While studying the Yixian weevil fauna and comparing it to those of other deposits of similar and older ages, it is transparent that serious problems remain in defining these fossil groups and incorporating them into the extant classification. For example, Zimmerman (1994) argued that Eobelidae Arnoldi (1977) was more closely related to Oxycorynidae and Belidae, likely a stem-group of Belidae. Gratshev and Zherikhin (2003) also believed that the Eobelidae, despite possibly comprising a polyphyletic group, was a stem lineage of modern Belidae. Alonso-Zarazaga and Lyal's (1999) classification, although not explicitly discussing any relationships, listed Eobelidae as a separate family. On the other hand, Kuschel (1983, 1994), Kuschel and Leschen (2011), Oberprieler *et al.* (2007), then Zherikhin (1986) and Gratshev and Zherikhin (1995, 1996) all have argued that Eobelidae constitute an extinct lineage of nemonychids. Similarly, Legalov (2009a,b, 2010a,b) maintained that Eobelidae are a basal (stem), polyphyletic lineage within Nemonychidae. According to the results of this study, aside from the controversy on where it should be placed, Eobelidae do not appear to be present in the Early Cretaceous of Yixian.

Regarding Eccoptarthridae, it has been a confusing mix of taxa to comprehend, to say the least. Not only has its taxonomic placement been ambiguous, its composition has also been confused. While many specimens have been attributed to this family, such as those treated from Yixian in this paper, as already mentioned, they appear to not actually belong to this group. Although superficially similar, *Eccoptarthrus crassipes* Arnoldi (1977) shares more synapomorphies with the eobelid lineage and to Nemonychidae in a broad sense (including the fossil eobelids), and other specimens, such as those in *Abrocar*, are likely also nemonychids (Oberprieler *et al.* 2007). Arnoldi (1977) described *Eccoptarthrus* as belonging in a subfamily (Oxycorynoidinae) within Eobelidae. Subsequent authors, such as Alonso-Zarazaga and Lyal (1999) and Liu and Ren (2006, 2007), have included Carinae and Baissorhynchinae as members of Eccoptarthridae. As demonstrated here, however, at least the Baissorhynchina probably belong to a more broadly defined Caridae (as alluded to by Kuschel 1983), and Eccoptarthridae (likely synonymous with Eobelidae) are likely members of a broader nemonychid clade (Legalov 2009a, 2010a,b), as also supported by Kuschel and Leschen (2011) who define Eobelinae as a subfamily within Nemonychidae.

*Implications towards weevil classification*:

Although the Yixian assemblage represents only a small fraction of the early weevil faunal composition, it provides much information on distributions and the early evolution of weevil clades. As mentioned before, although Eobelinae and Ulyanidae (also probably a lineage of Nemonychidae) have been found at the Karatau site, these groups have yet to be found at Yixian, and may be absent entirely, possibly signifying a different paleoenvironment of the Yixian and/or a greater antiquity of these two lineages. Similarly to the Karatau site, though, apparently extinct taxa of Nemonychidae are abundant, emphasizing the greater diversity of this clade during the Late Jurassic and Early Cretaceous. Due to the many extinct groups that appear to fall within Nemonychidae and adjacent to it, broader definitions of this clade and others will need to be redefined and tested against other classificatory hypotheses (Legalov 2009a, 2009b, 2009c, 2010a, 2010b; Alonso-Zarazaga and Lyal 1999). Indeed, placement of these fossils is quite difficult owing to the lack of well-established character systems outlining several extant weevil lineages. Because of this lack of information, many fossil weevil groups have been described based on relative gestalt, relying upon superficial similarity or characters that are unable to be informative of their proposed relationships, thus creating a great disparity in the classification between fossil and extant taxa. Also, as a result of relying upon such superficiality, many specimens are described as new or assigned to certain groups depending on their orientation. For example, dorsally-preserved specimens may have the same or similar traits to laterally preserved ones but are not visible in that orientation, and are so assigned to miscellaneous groups that are sometimes quite different. These challenges are compounded by the fact that few modern authors have elected to examine older type material (e.g., the numerous taxa described by Arnoldi from the Mesozoic of Asia), relying instead on the original descriptions and figures which are now known to be absolutely misleading (Davis pers. obs., in prep.). Although the results presented here are preliminary, a reclassification will certainly be necessary, particularly in light of the numerous Mesozoic nemonychid and nemonychid-like fossils described from Karatau (Kazakhstan; Arnoldi *et al.* 1977; Legalov 2010a, 2010b, 2010c; Gratshev and Legalov 2011), El Montsec (Spain; Gratshev and Zherikhin 2000a; Soriano *et al.* 2006; Zherikhin and Gratshev 1997), and various deposits in Mongolia (Zherikhin and Gratshev 2004; Legalov 2010b), as well as from New Jersey amber (Gratshev and Zherikhin 2000b). Of particular interest will be to examine the placement of the numerous groups comprising the Jurassic Eobelinae, as there appear to be many (convergent or plesiomorphic) characters shared with it and the Yixian stem groups (Davis, in prep.). Examination of these other groups will also resolve incongruent hypotheses of classification that currently exist. For example, according to Legalov (2009a), the Baissorhynchinae belong either in Caridae (when interpreting Ithyceridae in the strict sense) or in Ithyceridae *s.l.*, whereas they are included in Eccoptarthridae Arnoldi, 1977, according to Alonso-Zarazaga and Lyal (1999). It should again be emphasized that while several classificatory hypotheses have been proposed incorporating the fossil material mentioned in this study, they are largely based on original descriptions and illustrations that often display significant errors. Thus, re-examination of holotypes and undescribed material (as done here) is of utmost importance particularly in correctly assessing fossil taxa and incorporating them into classificatory hypotheses. Lastly, it is hoped that with the continued detailed description of more fossil groups, such as those from the Yixian, and comparing character systems of both fossil and extant groups, the classification of Curculionoidea may reach greater stability and become of more practical use.

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**Figure legends**:

**Figure 1**. A-B, *Eccoptarthrus crassipes* Arnoldi (holotype), PIN 2239-1507. A, photomicrograph; B, illustration. C-D, *Eobelus longipes* Zherikhin (holotype), PIN 2452-275. C, photomicrograph; D, illustration, showing linear ventral connection of rostrum and cranium. E-F, *Eobelus* sp., PIN 2384-516. E, photomicrograph; F, illustration, showing sensory setae at apex of labrum.

**Figure 2**. A-B, *Baissorhynchus tarsalis* Zherikhin (holotype), PIN 1989-3010. A, photomicrograph; B, illustration. C-F, undescribed compressions of *Baissorhynchus* spp. from Baissa. C-D, PIN 4210-727. C, photomicrograph; D, illustration, showing elongated antennal scape. E-F, PIN 3064-7219. E, photomicrograph; F, illustration, showing single (fused) gular suture. G-H, undescribed compression of *Cretonanophyes* sp. from Karatau (original part). G, photomicrograph; H, illustration.

**Figure 3**. A-C, undescribed compression of *Cretonanophyes* sp. from Karatau (counterpart of 2G). A, photomicrograph; B, illustration, showing single (fused) gular suture; C, enlargement of cranium in A. D-F, *Cretonanophyes longirostrus* Zherikhin (holotype), PIN 1668-1772. D, photomicrograph; E, specimen illustration; F, photomicrograph enlargement of legs and tarsi. G-J, extant *Car* sp., photomicrographs. G, adult, lateral aspect; H, protibia, showing dense protibial setal patch; I, protarsus, showing expanded basitarsomere; J, meso- and metanota.

**Figure 4**. A-H, *Cretonanophyes punctatus* Liu and Ren. A-B, CNC-C-LB2006103 (holotype). A, photomicrograph; B, illustration. C-D, CNU-C-LB2007105-2. C, photomicrograph; D, illustration, indicating similar form of metascutum to extant Caridae. E-F, CNC-C-LB2005115. E, photomicrograph; F, illustration, showing single gular suture. G-H, CNU-C-LB2010707. G, photomicrograph; H, illustration.

**Figure 5**. A-B, *Cretonanophyes punctatus* Liu and Ren, CNU-C-LB2010708. A, photomicrograph; B, illustration. C-H, *Cretonanophyes zherikhini* Liu and Ren. C-F, holotype (original part and counterpart). C-D, CNU-C-LB2005103 (original part). C, photomicrograph; D, illustration, showing protibial brush. E-F, CNU-C-LB2005104 (counterpart). E, photomicrograph; F, illustration. G-H, CNU-C-LB2005109. G, photomicrograph; H, illustration, showing similar form of metascutum to extant Caridae single gular suture.

**Figure 6**. A-F, *Cretonanophyes zherikhini* Liu and Ren. A-B, CNC-C-LB2005112. A, photomicrograph; B, illustration, showing single gular suture. C-D, CNC-C-LB2005114. C, photomicrograph; D, illustration. E-F, CNC-C-LB2006101. E, photomicrograph; F, illustration, showing protibial brush. G-H, *Abrocar brachyorhinos* Liu and Ren, CNU-C-LB2005105 (holotype). G, photomicrograph; H, illustration.

**Figure 7**. A-H, *Abrocar brachyorhinos* Liu and Ren. A-B, CNU-C-LB2005125. A, photomicrograph; B, illustration. C-D, CNU-C-LB2005119. C, photomicrograph; D, illustration. E-H, original part & counterpart. E-F, CNU-C-LB2010701 (original part). E, photomicrograph; F, illustration. G-H, CNU-C-LB2010703 (counterpart). G, photomicrograph; H, illustration.

**Figure 8**. A-D, *Abrocar brachyorhinos* Liu and Ren (original part & counterpart). A-B, CNU-C-LB2010705 (original part). A, photomicrograph; B, illustration. C-D, CNU-C-LB2010706 (counterpart). C, photomicrograph; D, illustration. E-H, *Abrocar macilentus* Liu and Ren. E-F,

CNU-C-LB2006102 (holotype). E, photomicrograph; F, illustration. G-H, CNU-C-LB2005110. G, photomicrograph; H, illustration.

**Figure 9**. A-F, *Abrocar macilentus* Liu and Ren. A-B, CNU-C-LB2007103. A, photomicrograph; B, illustration. C-D, CNU-C-LB2010156. C, photomicrograph; D, illustration. E-F, CNU-C-LB2010704. E, photomicrograph; F, illustration. G-H, *Abrocar concavus* new species, CNU-C-LB2007105, original part (holotype). G, photomicrograph; H, illustration, showing depression in pronotum.

**Figure 10**. A-B, *Abrocar concavus* new species, CNU-C-LB2007105, counterpart (holotype). A, photomicrograph; B, illustration, showing depression in pronotum. C-H, *Abrocar relicinus* new species. C-D, CNU-C-LB2010152 (holotype). C, photomicrograph; D, illustration. E-F, CNU-C-LB2005116 (original part). E, photomicrograph; F, illustration. G-H, CNU-C-LB2005122. G, photomicrograph; H, illustration.

**Figure 11**. A-B, Abrocarina Gen. sp. indeterminate 1, CNU-C-LB2010154. A, photomicrograph; B, illustration. C-D, *Brenthorrhinoides mandibulatus* Gratshev and Zherikhin (holotype), PIN 2239-1508. C, photomicrograph; D, illustration. E-H, *Chinocimberis angustipecteris* (Liu, Ren, and Tan). E-F, CNU-C-LB2005102 (holotype). E, photomicrograph; F, illustration, showing details of the metanotum. G-H, CNU-C-LB2005127. G, photomicrograph; H, illustration, indicating the presence of paired gular sutures.

**Figure 12**. A-B, *Chinocimberis angustipecteris* (Liu, Ren, and Tan), CNU-C-LB2007104. A, photomicrograph; B, illustration, showing details of the metanotum. C-H, *Chinocimberis magnoculi* (Liu, Ren, and Tan). C-F, original part & counterpart (holotype). C-D, CNU-C-LB2005107, original part (holotype). C, photomicrograph; D, illustration, showing paired gular sutures. E-F, CNU-C-LB2005108, counterpart (holotype). E, photomicrograph; F, illustration. G-

H, CNU-C-LB2010155. G, photomicrograph; H, illustration, showing details of thoracic lateral sclerites.

**Figure 13**. A-B, *Chinocimberis magnoculi* (Liu, Ren, and Tan), CNU-C-LB2010702. A, photomicrograph; B, illustration. C, *Mecomacer scambus*, metanotum, photomicrograph. D-I, *Renicimberis latipecteris* (Liu, Ren, and Tan). D-E, CNU-C-LB2005101 (holotype). D, photomicrograph; E, illustration, showing details of the metanotum and paired gular sutures. F-G, CNU-C-LB2007101. F, photomicrograph; G, illustration. H-I, CNU-C-LB2005123. H, photomicrograph; I, illustration.

**Figure 14**. A-B, *Renicimberis latipecteris* (Liu, Ren, and Tan), CNU-C-LB2010153. A, photomicrograph; B, illustration, showing paired gular sutures. C-F, *Microprobelus liuae* Liu, Ren, and Shih. C-D, CNU-C-LB2005106 (holotype). C, photomicrograph; D, illustration. E-F, CNU-C-LB2007102. E, photomicrograph; F, illustration.

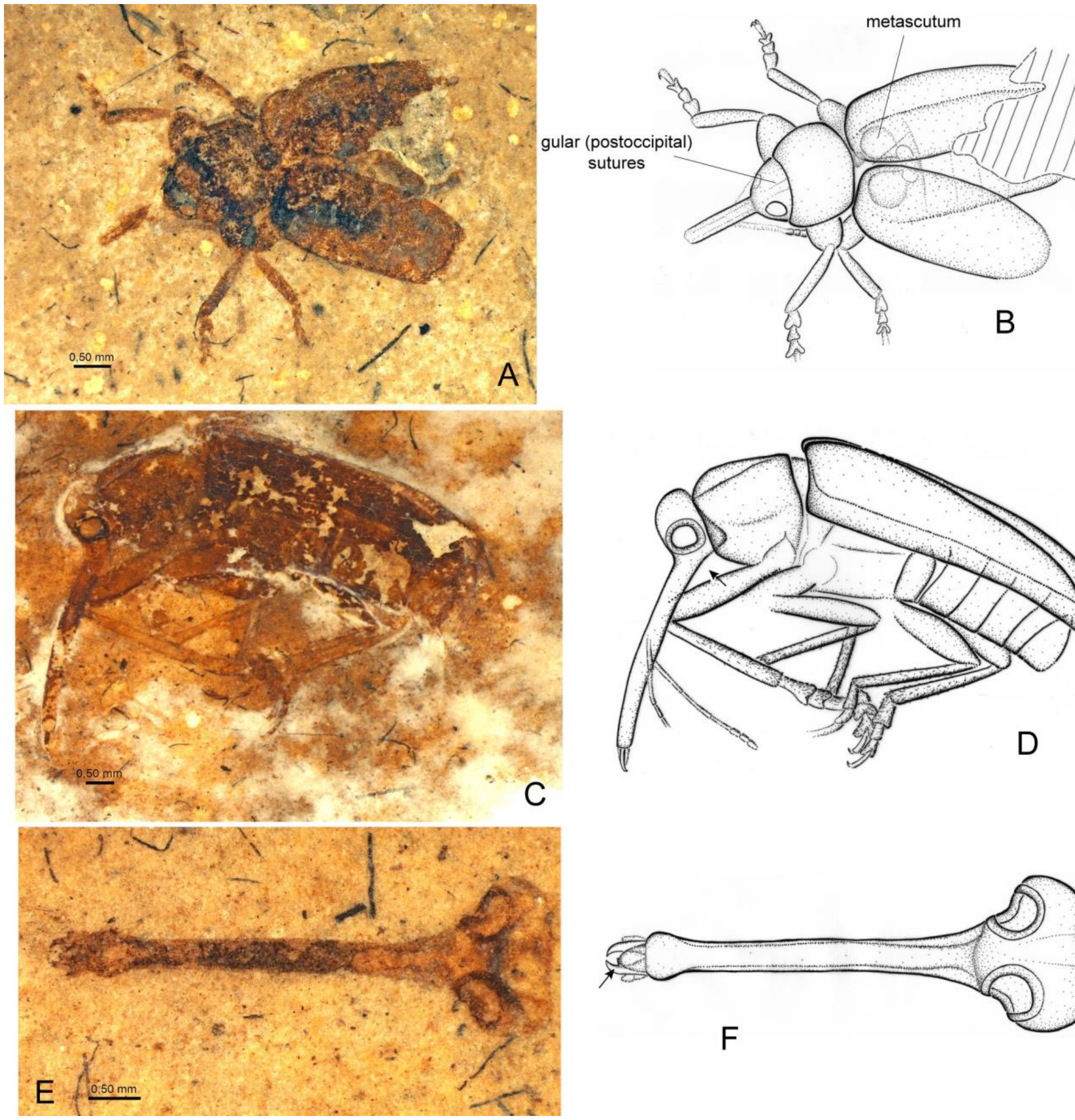
**Figure 15**. A-E, *Dicordylus marmoratus*, photomicrographs. A, meso- and metanota; B, proleg, showing protibial brush; C, protarsus, showing enlarged basitarsomere; D-E, metaleg, showing longitudinal crenulate ridge on outer margin of tibia. D, dorsal aspect; E, lateral aspect. F-G, Family *Incertae Sedis* gen. sp. indeterminate 2, CNU-C-LB2005111. F, photomicrograph; G, illustration. H-I, Family *Incertae Sedis* gen. sp. indeterminate 3. H, photomicrograph; I, illustration.

**Figure 16**. A-F, Family Nemonychidae? gen. sp. indeterminate 4, CNU-C-LB2007104-2 (original part & counterpart). A-B, original part. A, photomicrograph; B, illustration. C-D, counterpart. C, photomicrograph; D, illustration. E-F, CNU-C-LB2010709. E, photomicrograph; F, illustration. G-H, Family Anthribidae? gen. sp. indeterminate 5, CNU-C-LB2005126. G, photomicrograph; H, illustration. I-J, *Phaenithon semigriseum*, photomicrographs. I, posterior

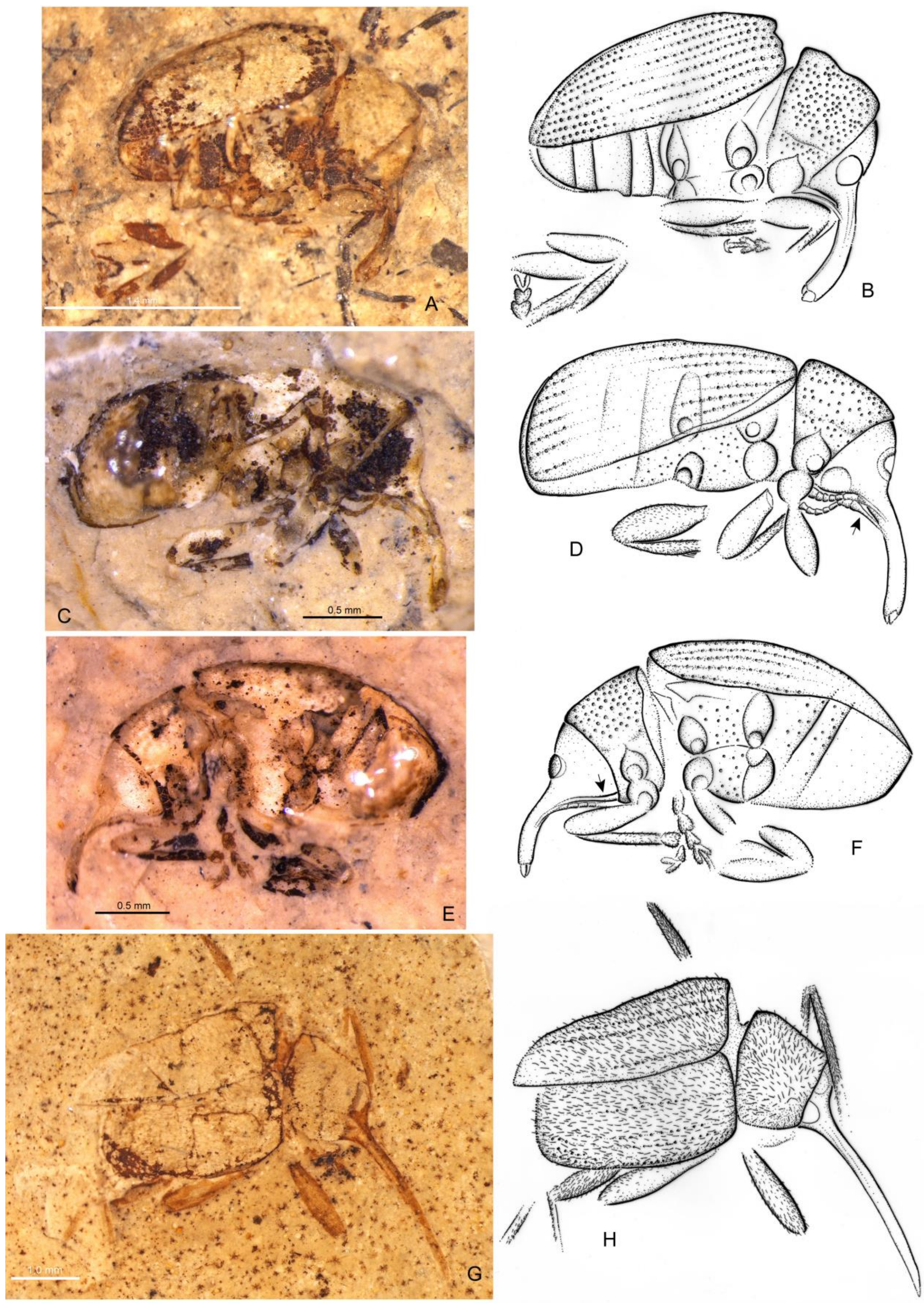
end of adult, showing elongated tergite 7 and elytra that extend only to basal part of tergite (lateral aspect); J, middle region of adult, showing posterior part of pronotum, prebasal transverse carina on the pronotum, and anterior region of elytra (lateral aspect).

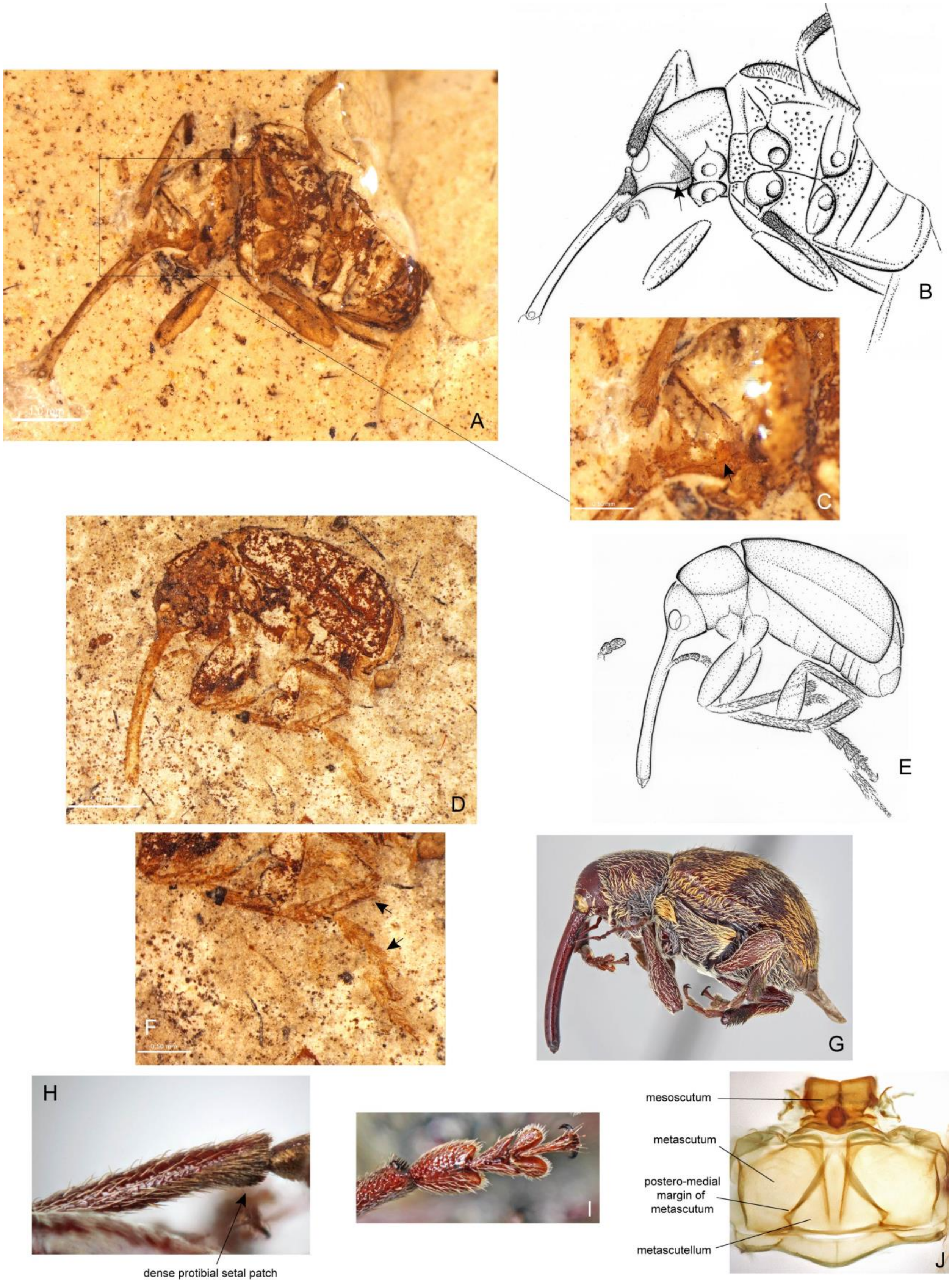
**Table 1**. Summary table of Yixian weevil fauna as recognized by this study.

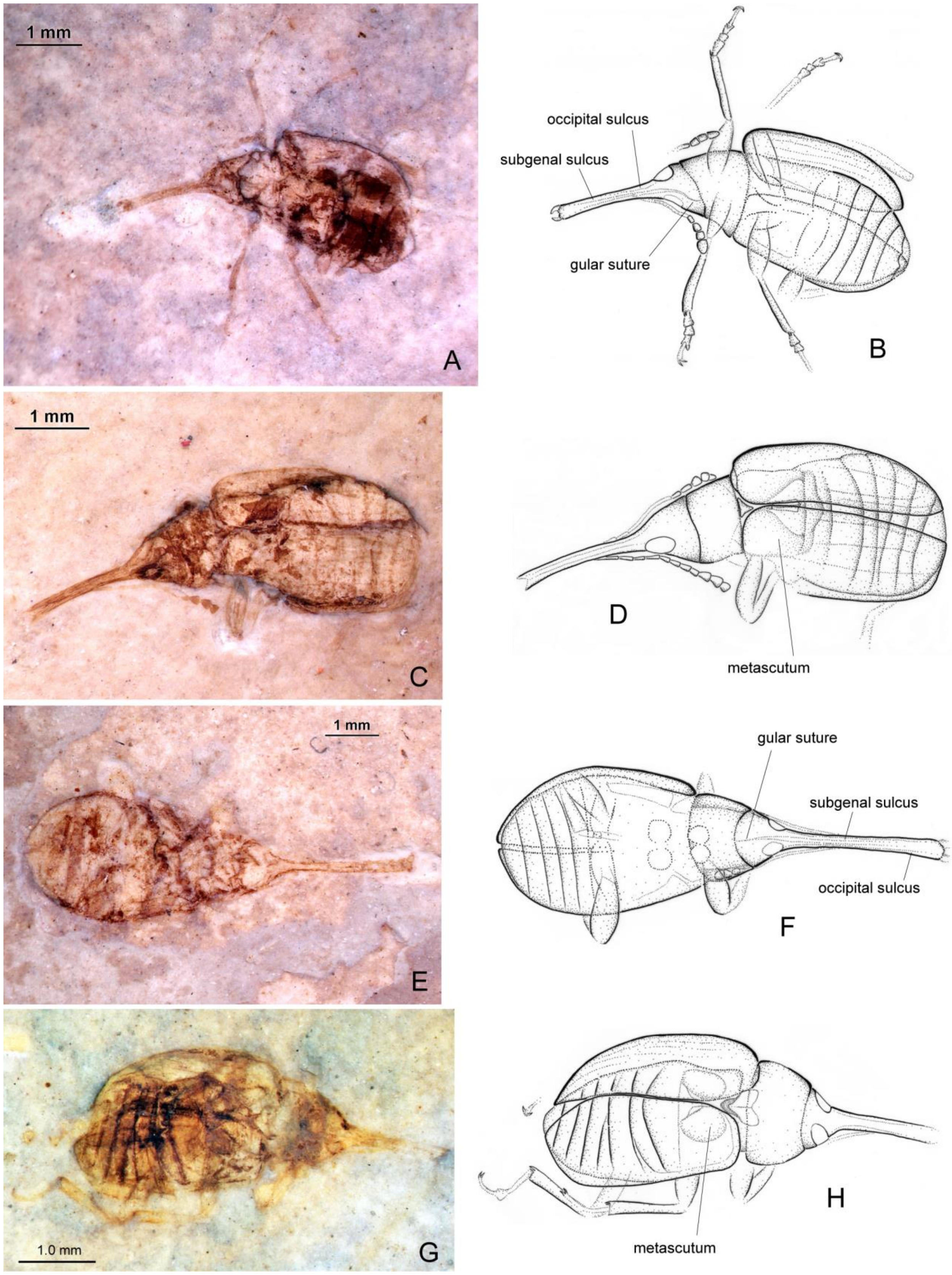
| |
|---|
| Family ***Incertae Sedis*** |
| Tribe **Baissorhynchini** Zherikhin |
| Subtribe **Baissorhynchina** Zherikhin |
| ***Cretonanophyes punctatus*** Liu and Ren, **resurrected combination** |
| ***Cretonanophyes zherikhini*** Liu and Ren, **resurrected combination** |
| |
| Subtribe **Abrocarina** Legalov |
| ***Abrocar brachyorhinos*** Liu and Ren |
| ***Abrocar macilentus*** Liu and Ren |
| ***Abrocar concavus***, **new species** |
| ***Abrocar relicinus***, **new species** |
| **Gen. sp.? indeterminate 1** |
| |
| Family **Nemonychidae** Bedel |
| Subfamily **Cimberidinae** Gozis |
| Tribe **Cimberidini** Gozis |
| ***Chinocimberis angustipecteris*** (Liu, Ren, and Tan) |
| ***Chinocimberis magnoculi*** (Liu, Ren, and Tan) |
| ***Renicimberis latipecteris*** (Liu, Ren, and Tan) |
| |
| Family **Belidae**? Schönherr |
| ***Microprobelus liuae*** Liu, Ren, and Shih |
| |
| Family ***Incertae Sedis*** |
| **Gen. sp. indeterminate 2** |
| **Gen. sp. indeterminate 3** |
| |
| Family **Nemonychidae**? Bedel |
| **Gen. sp. indeterminate 4** |
| |
| Family **Anthribidae**? Billberg |
| **Gen. sp. indeterminate 5** |



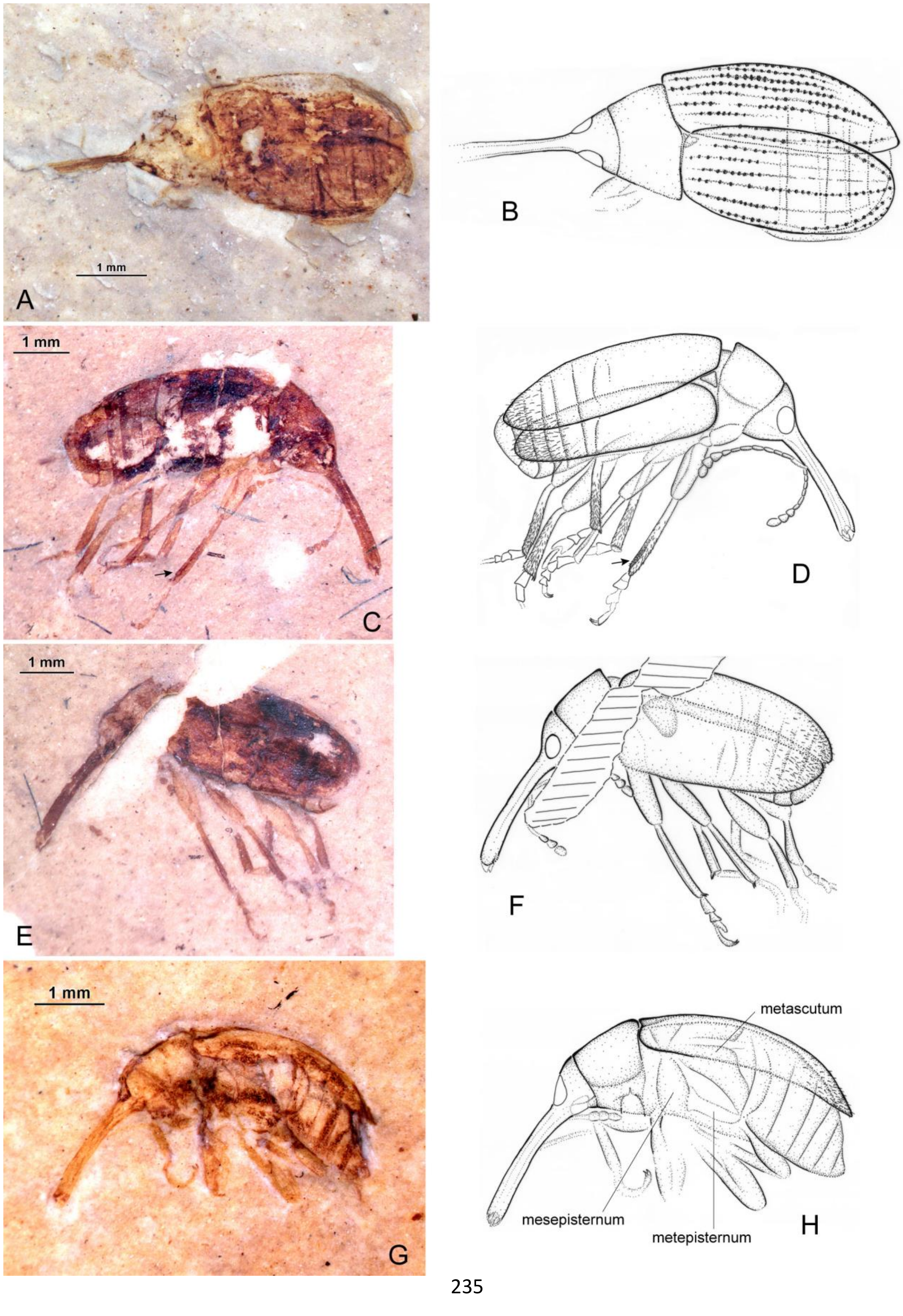
0,50 mm
A
metascutum
gular (postoccipital)
sutures
B
0,50 mm
C
D
E
0,50 mm
F

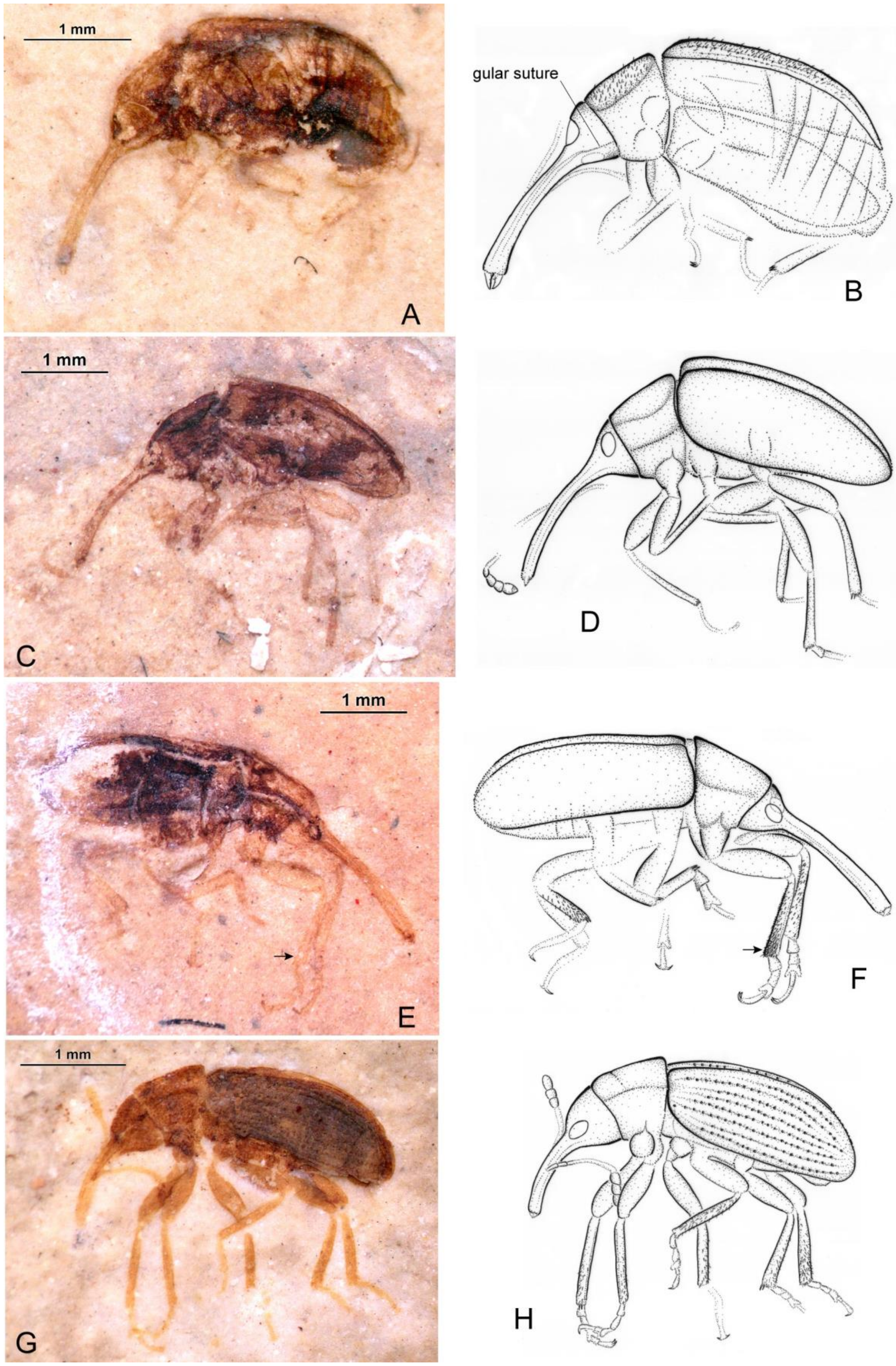

A
B
C
0,5 mm
D
E
0.5 mm
F
G
1.0 mm
H

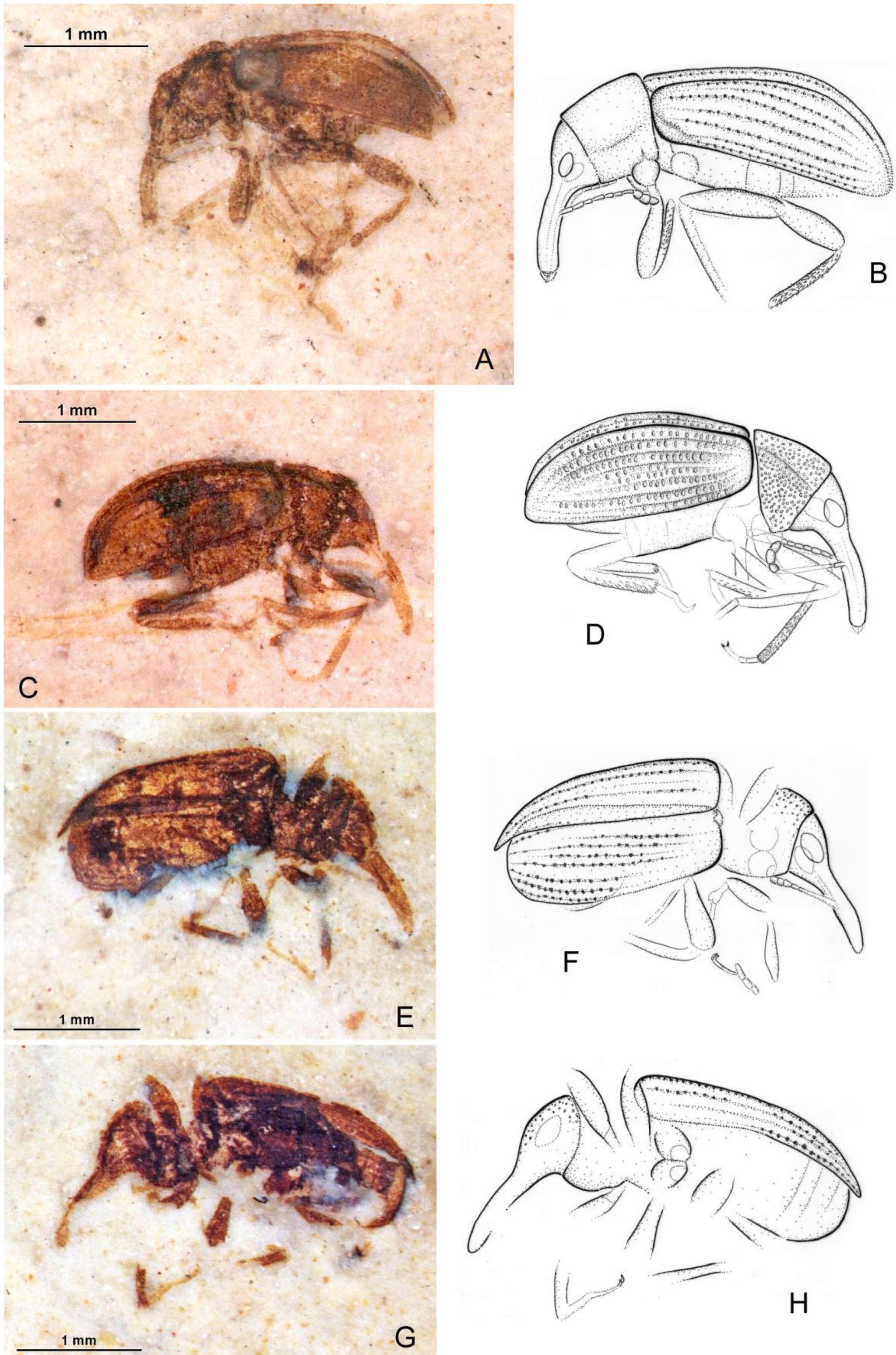

A
B
C
D
E
F
G
H
dense protibial setal patch
I
mesoscutum
metascutum
postero-medial margin of metascutum
metascutellum
J

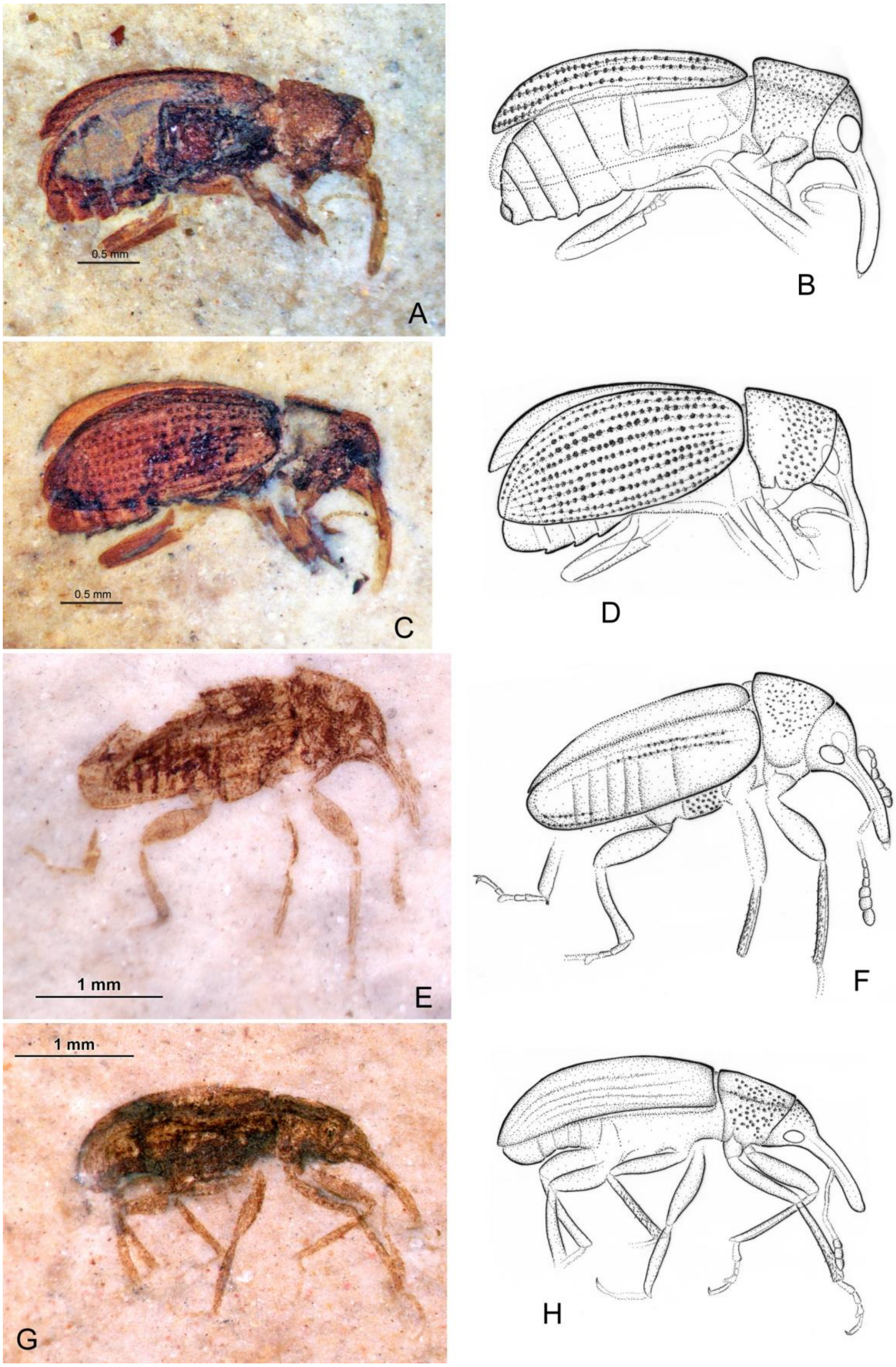


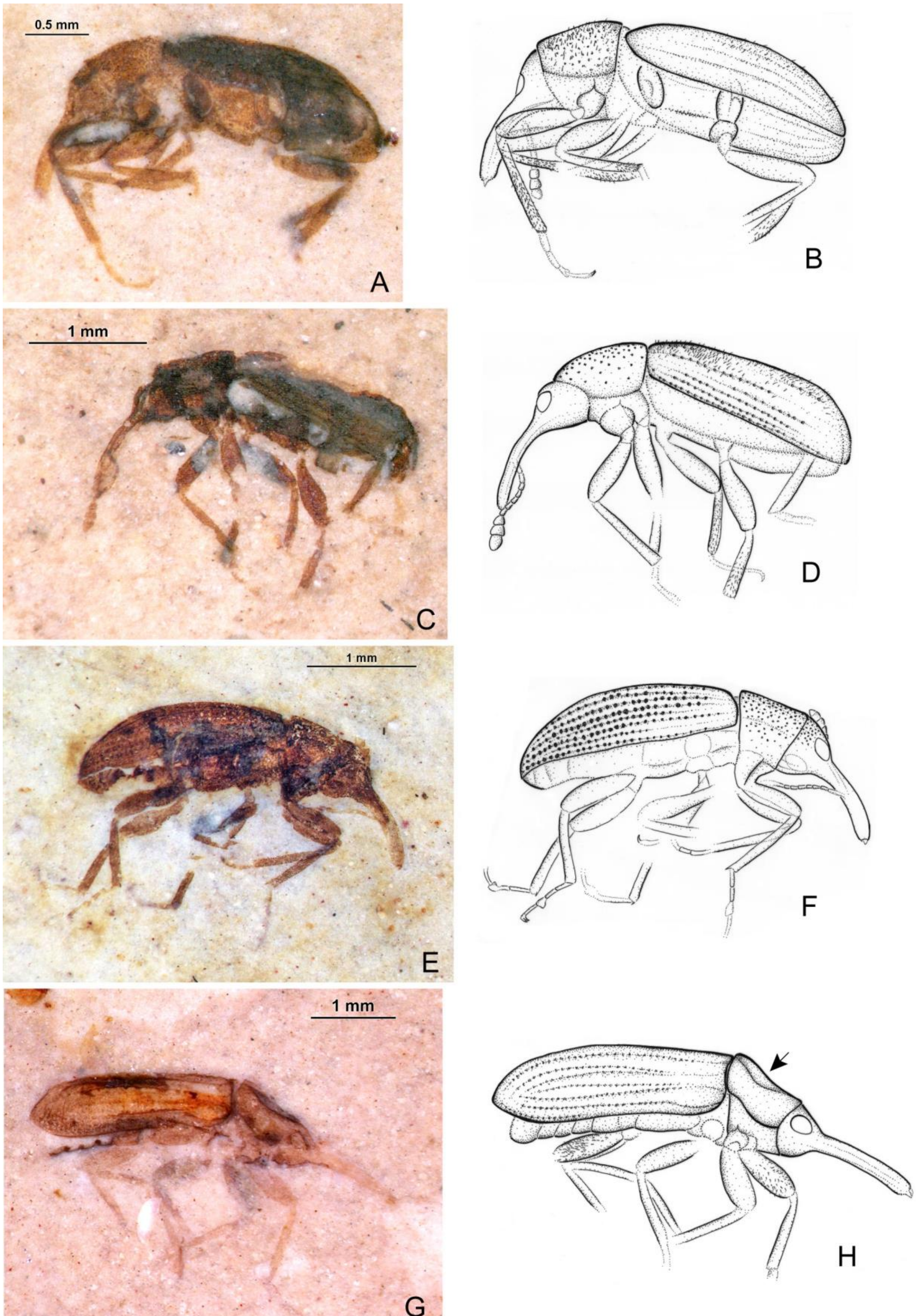
1 mm
A
occipital sulcus
subgenal sulcus
gular suture
B
1 mm
C
D
metascutum
1 mm
E
gular suture
subgenal sulcus
occipital sulcus
F
1.0 mm
G
H
metascutum

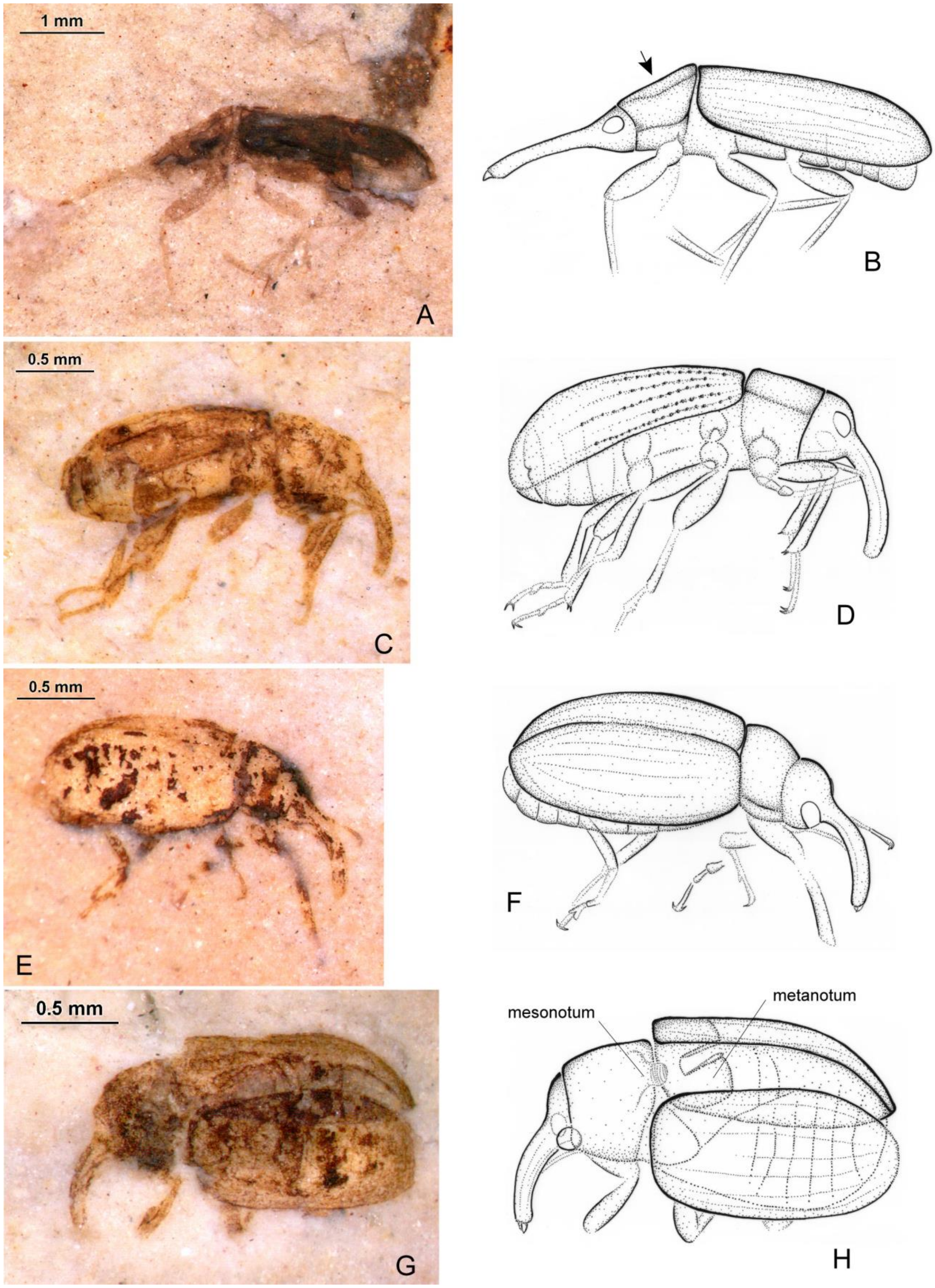

1 mm
A
B
1 mm
C
D
1 mm
E
F
1 mm
G
metascutum
mesepisternum
metepisternum
H

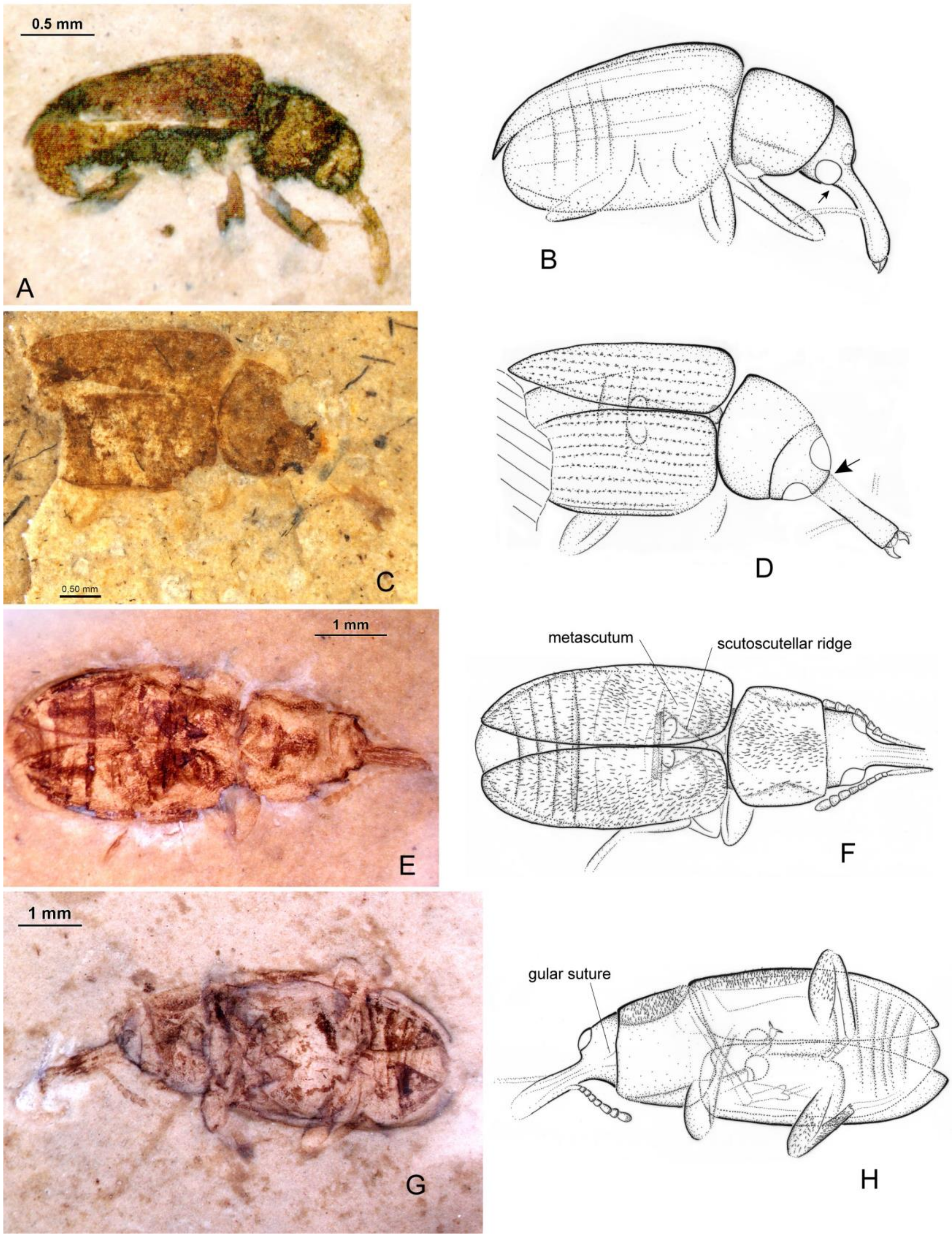

1 mm
A
gular suture
B
1 mm
C
D
1 mm
E
F
1 mm
G
H

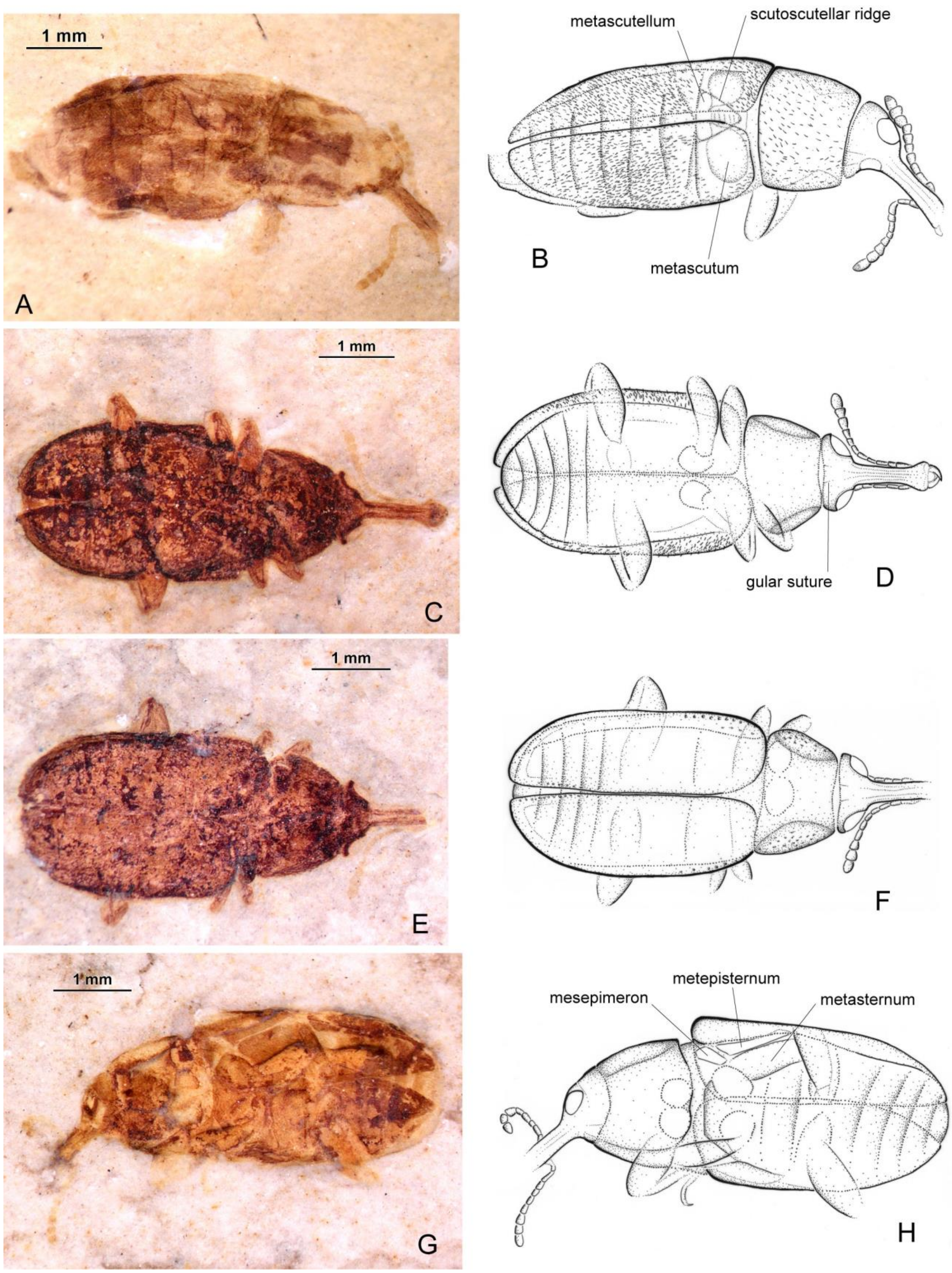

1 mm
A
B
1 mm
C
D
E
1 mm
F
G
1 mm
H

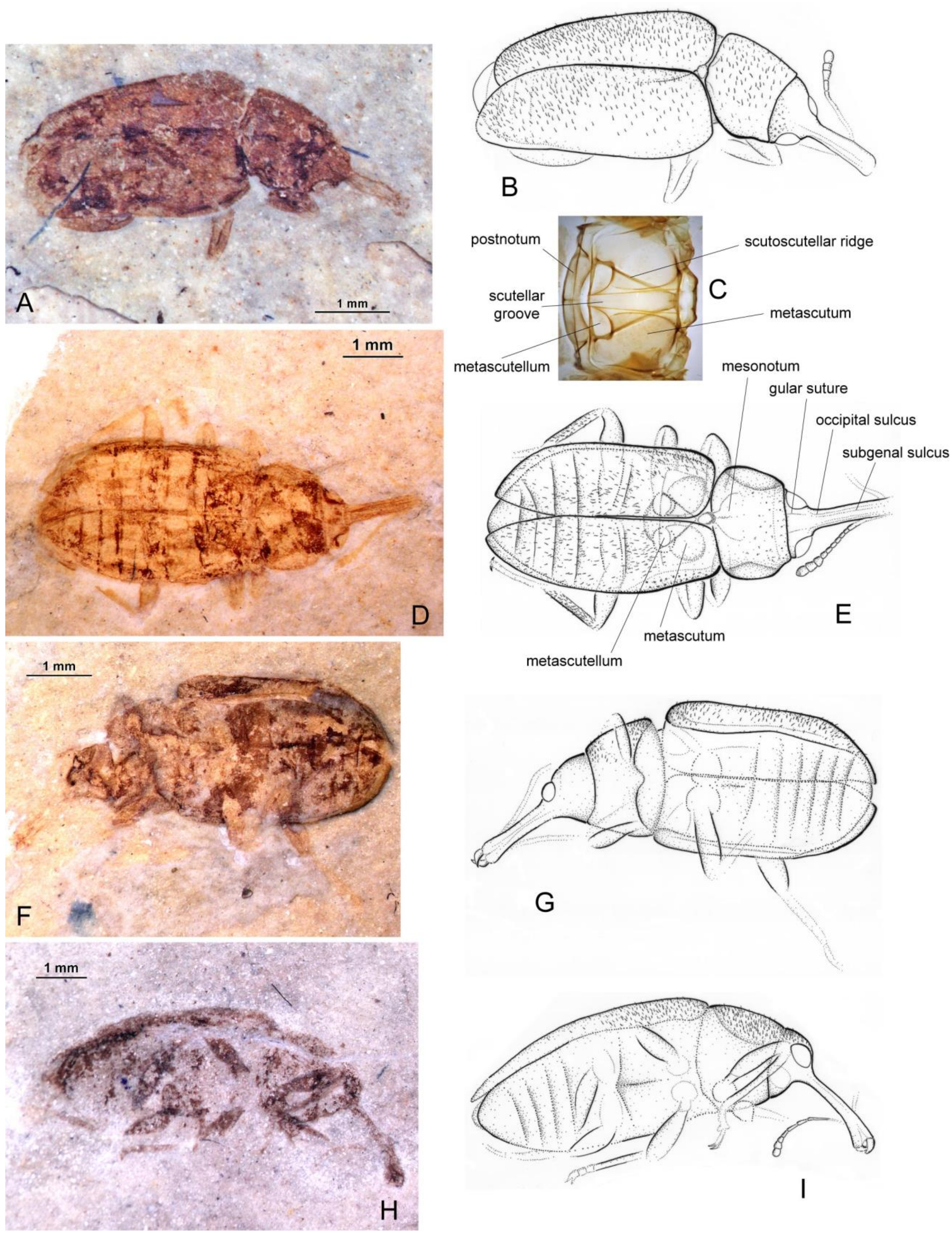

0.5 mm
A
B
0.5 mm
C
D
1 mm
E
F
1 mm
G
H


0.5 mm
A
B
1 mm
C
D
1 mm
E
F
1 mm
G
H

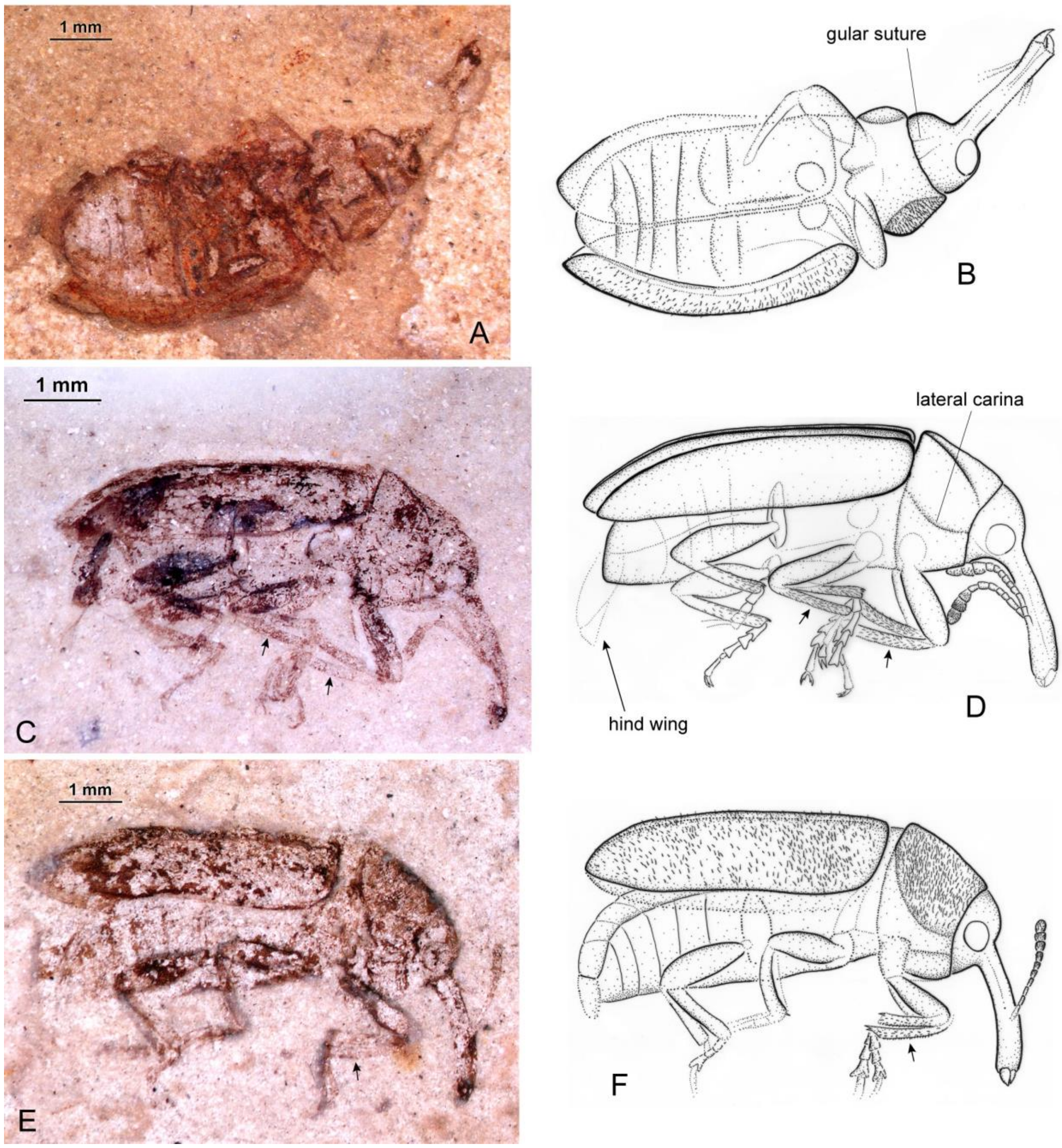

1 mm
A
B
0.5 mm
C
D
0.5 mm
E
F
0.5 mm
mesonotum
metanotum
G
H

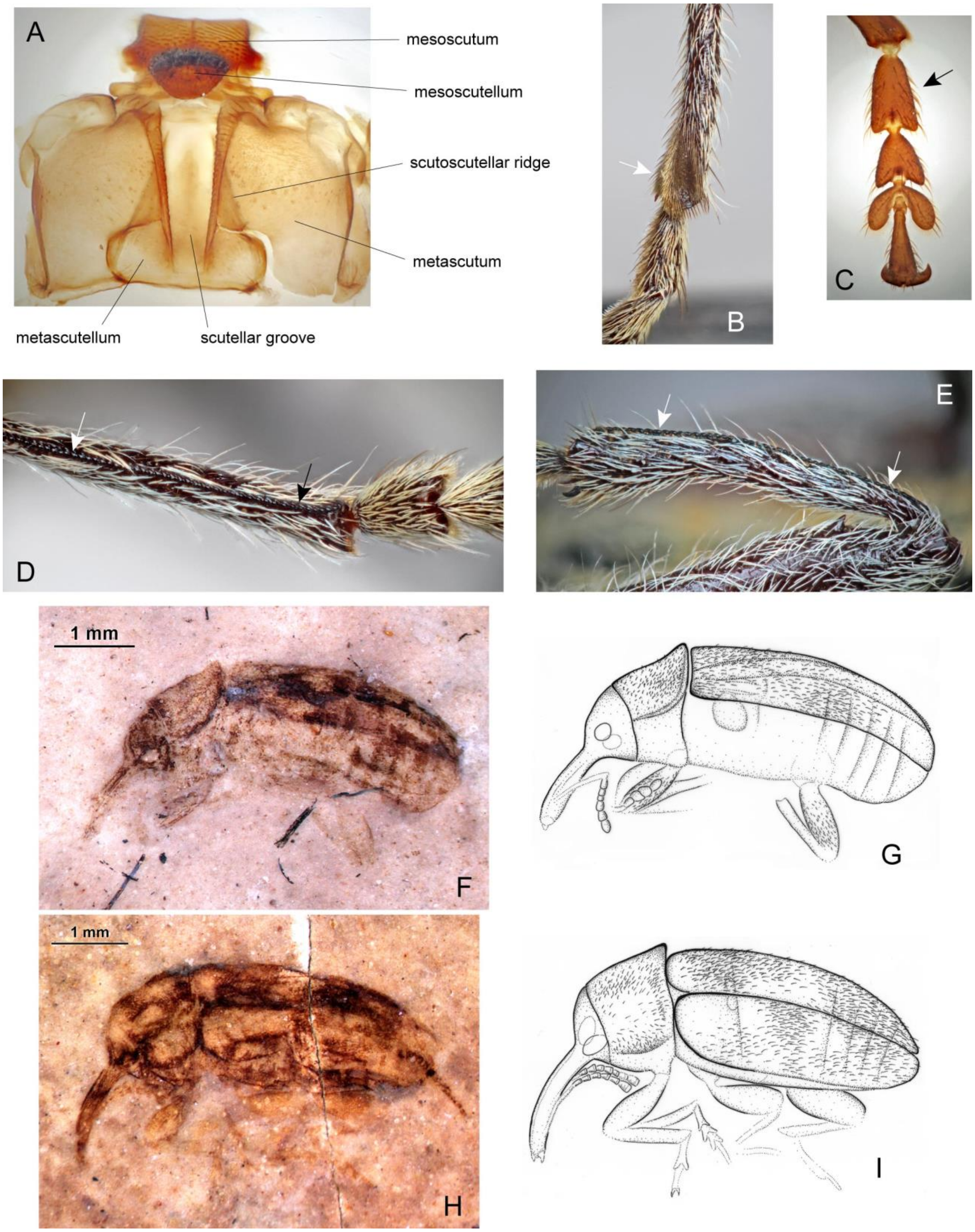

0.5 mm
A
B
C
0,50 mm
D
1 mm
E
metascutum
scutoscutellar ridge
F
1 mm
G
gular suture
H

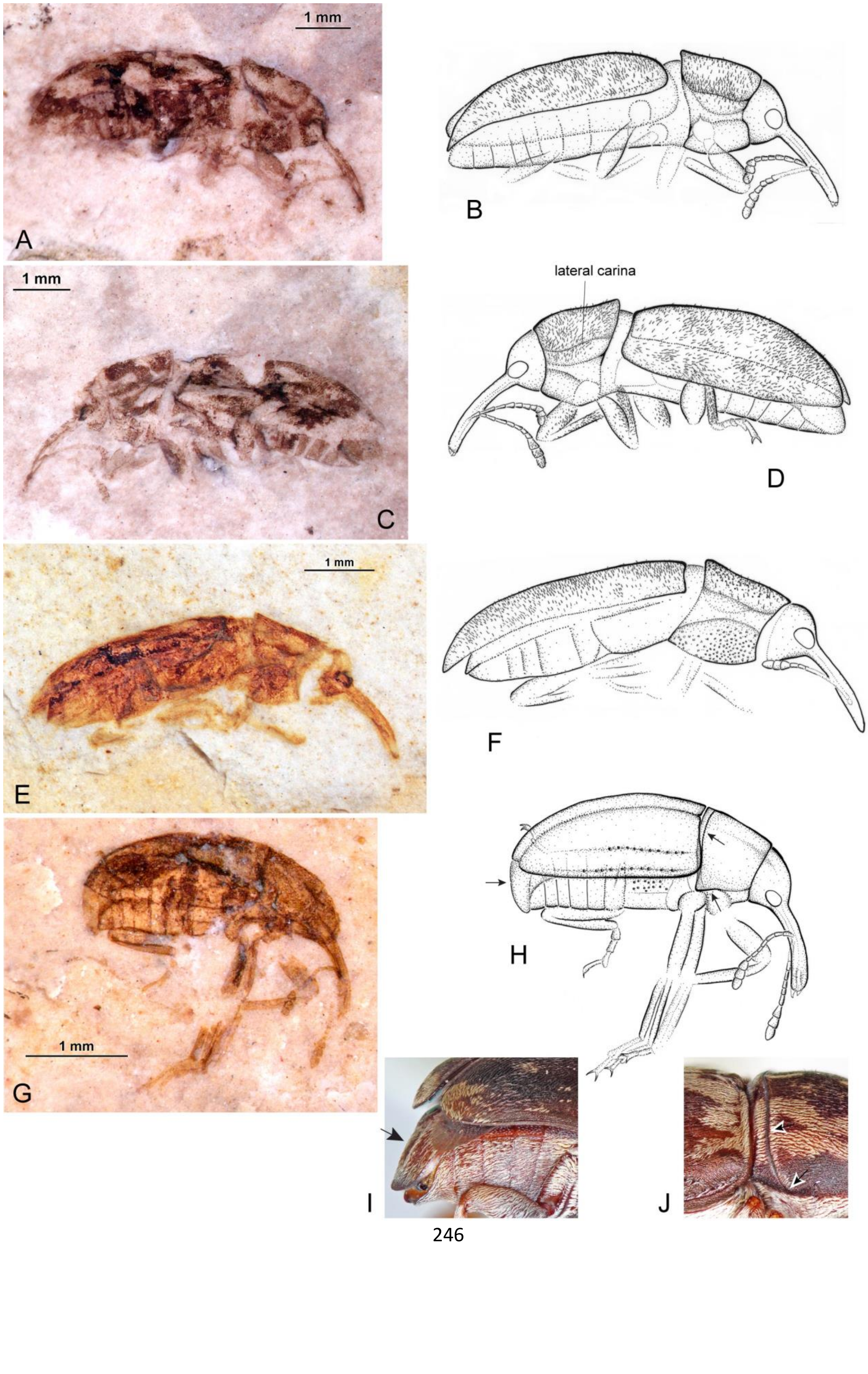

1 mm
A
metascutellum
scutoscutellar ridge
metascutum
B
1 mm
C
gular suture
D
1 mm
E
F
1 mm
G
mesepimeron
metepisternum
metasternum
H



A
1 mm
B
postnotum
scutoscutellar ridge
scutellar groove
C
metascutum
metascutellum
1 mm
D
mesonotum
gular suture
occipital sulcus
subgenal sulcus
E
metascutum
metascutellum
1 mm
F
G
1 mm
H
I


1 mm
A
gular suture
B
1 mm
C
lateral carina
hind wing
D
1 mm
E
F


A
mesoscutum
mesoscutellum
scutoscutellar ridge
metascutum
metascutellum
scutellar groove
B
C
D
E
1 mm
F
G
1 mm
H
I



1 mm
A
B
1 mm
lateral carina
C
D
1 mm
E
F
H
1 mm
G
I
J

## 3. Phylogeny and classification of Caridae Thompson, 1992 (Coleoptera: Curculionoidea) with descriptions of new taxa from Burmese amber

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**Abstract**

A revised classification of Caridae Thompson (1992) is presented based on the first phylogenetic analysis of this lineage and related groups using morphological character data. In order to accomplish such a task and be as thorough as possible, all extant and fossil genera were included. As is now evident from the fossil record and several new specimens discovered in Burmese amber, carids were more abundant and diverse in the Cretaceous, though this diversity has gone largely unrecognized due to difficulties in associating fossil taxa with extant faunal lineages. In order to more fully characterize this family, character data were extracted from as many regions of the adult body as possibly. The following taxa from Burmese amber are described as new: *Zigras cornus* **sp. nov.**, *Z. nudicornus* **sp. nov.**, *Scabridus zigrasi* **sp. nov.**, and *S. asperum* **sp. nov.** *Hispanocar* Soriano *et al*. is here considered a junior synonym of *Cretonanophyes* Zherikhin, and the following taxonomic changes are made: C*retonanophyes edmundi* (Zherikhin & Gratshev) **n. comb.** and C*retonanophyes kseniae* (Soriano *et al*.) **n. comb.**

**Keywords**: amber, compression fossils, Cretaceous, weevils, Eccoptarthridae

## Introduction

Caridae has long been a rather anomalous weevil group, interesting both for its life history characteristics and morphology. While the majority of weevil families can be rather quickly ascribed to either more primitive or more derived phylogenetic positions, Caridae display characteristics of a somewhat intermediate spectrum. While they retain the ancestral host association with conifers, in which the larvae retain the plesiomorphic feature of thoracic legs, they represent one of the earliest groups to evolve an elongated antennal scape. This condition permits the antennae to fold more posteriorly on the head at the pedicel while maintaining sensory function and some motility, allowing the rostrum to reach greater depths while drilling oviposition holes in plant tissues. The other groups to independently evolve this feature include representatives in Brentidae (Nanophyinae and some Apioninae) and Curculionidae, the family predominantly known for the oviposition rostrum. Although Caridae and Brentidae also have developed this geniculate antennal form, it is fundamentally different at the scape-pedicel point of articulation. While the acetabulum of the scape for reception of the condyle of the pedicel is located apically in Caridae and Brentidae (as in all weevils with orthocerous antennae), the position of this acetabulum shifts laterally in all Curculionidae, thus producing a truly geniculate antenna.

As many features in Caridae are quite similar to those found in several other weevil families, such as Brentidae, Belidae, and Attelabidae, previous classifications have placed the group within or near these respective hierarchies (e.g., Kuschel 2003, Marvaldi & Morrone 2000, Marvaldi *et al.* 2002, May 1993, Oberprieler *et al.* 2007, Thompson 1992, Zherikhin & Gratshev 1995, Zimmerman 1994). Morphological characters of some contention due to their homoplasious condition include an elongated antennal scape, crenulate carinae along the dorsal femoral and tibial margins, and enlarged first tarsomeres. As a result of this study, Caridae is found to be sister to Ithyceridae + Brentidae + Curculionidae *sensu lato* (including Brachyceridae, Erirhinidae, Raymondionymidae, and possibly Scolytidae + Platypodidae).

**Materials and methods**

The amber pieces were excavated from the strata in the northern state of Kachin in Myanmar as part of regular and ongoing mining operations and is from the collection of Mr. James S. Zigras, available for study through the American Museum of Natural History (AMNH), New York. The origin, age, and fauna of Burmese amber have been reviewed by Grimaldi et al. (2002), Ross et al. (2010), and Shi *et al.* (2012), the latter of which arrived at an age of approximately 99 Ma (providing a range close to the Aptian-Cenomanian boundary). Due to the round surfaces of some of the pieces, glycerin was applied to a small coverslip and placed on the area directly above the inclusions in order to acquire more satisfactory viewing and photography. Photomicrographs were obtained by combining a z-stack of approximately 30 images using the computer software CombineZ. Illustrations were made through the aid of a drawing tube attached to an Olympus SZX9 stereomicroscope and using Adobe Illustrator CS3.

**Results**

Systematic Paleontology

Order **Coleoptera** Linnaeus, 1758

Suborder **Polyphaga** Emery, 1886

Infraorder **Cucujiformia** Lameere, 1938

Parvorder **Phytophaga** Dumeril, 1806

Superfamily **Curculionoidea** Latreille, 1802

Family **Caridae** Thompson, 1992

*Zigras* **gen. nov.**

Type species: *Zigras cornus* [as presently designated].

Diagnosis:

This genus is most easily recognized by the pair of short interocular tubercles on the head and a metafemoral tooth. Other features include strongly bulging compound eyes and antennae inserted approximately at the middle of the rostrum.

Etymology:

Patronym dedicated to Mr. James Zigras, who obtained all of the Burmese specimens herein and permitted their examination.

Comments:

This genus appears to share closest affinities to the new genus *Scabridus*, particularly in the elongated scape and antennae situated further from the base of the rostrum.

*Zigras cornus* **sp. nov.**

(Figs. 5-6)

Description:

Total body length (excluding rostrum): ca. 1.4 mm; maximal width (at elytral humeri): ca. 0.7 mm; elytral length: ca. 0.9 mm. Integument appearing dark brown to black. Scales absent, but dense covering of short setae along pronotum and elytra, sparser setae laterally on body and ventrally. Head with sparse, shallow punctures; constricted just before eyes. Compound eyes large and bulging, situated at base of rostrum. Rostrum approximately 1.2x as long as pronotum along middle, subequal in width along length; a pair of tuberculate horns between eyes at base of rostrum. Antennae inserted latero-ventrally, immediately after middle of rostrum, composed of scape, pedicel, funicle (flagellum) of 6 articles, and club of 3 articles; scape not reaching anterior margin of eye; pedicel and funicular articles short, moniliform; club loose, apical 3rd article conical, annulated at middle and appearing subdivided. Pronotum constricted anteriorly at collar, bearing dense, shallow punctures that are nearly confluent. Mesoscutellum not visible. Elytra with 10 shallowly punctured striae; sutural striole absent; interstices convex, each interstice with a densely and shallowly punctured stria; elytral shoulders prominent. Abdomen with pygidium (tergite VII) exposed, apical margin truncate; ventrite II with short spine protruding at middle near posterior margin. Ventral and lateral surface sparsely covered with shallow punctures. Legs with tibial spur formula 1-2-2; trochanters small, triangular. Forelegs elongate, longer than mid- and hindlegs; procoxae apparently touching, procoxal cavities open laterally with visible dorsal cleft; protibiae with an outer apical spine (uncus) and dense setal patch at inner apical angle; metafemora with inner, narrow spine at middle. Tarsi with article 1 rather narrow, not distinctly expanded; pretarsal claws (ungues) divaricate with inner subbasal swelling or lobe.

Holotype:

♂? Zigras 2, Myanmar: Kachin; Cretaceous: Early Cenomanian; in the private collection of Mr. James S. Zigras.

Paratype:

♂? Zigras 167, Myanmar: Kachin; Cretaceous: Early Cenomanian; in the private collection of Mr. James S. Zigras.

Etymology:

Specific epithet derived from the Latin *cornu* meaning "horn", referring to the conspicuous spine present on ventrite 2.

Comments:

This species is best recognized by the spine present on ventrite II. It should be recognized, however, that such a character could represent a sexual dimorphism and it is therefore possible that these specimens are males.

*Zigras nudicornus* **sp. nov.**

(Fig. 7)

Description:

Total body length (excluding rostrum): ca. 1.5 mm; maximal width (along middle of elytral): ca. 0.7 mm; elytral length: ca. 1.0 mm. Integument appearing dark brown to black. Scales absent, but dense covering of short setae along pronotum and elytra, sparser setae laterally on body and ventrally. Head not constricted before eyes. Compound eyes large and bulging, situated at base of rostrum. Rostrum approximately 0.8x as long as pronotum along middle, slightly widening apically; a small, short pair of tuberculate horns between eyes at base of rostrum. Antennae inserted laterally, immediately after middle of rostrum, composed of scape, pedicel, funicle (flagellum) of 6 articles, and club of 3 articles; scape not reaching anterior margin of eye; pedicel and funicular articles short, moniliform; club loose, apical 3rd article conical, annulated at middle and appearing subdivided. Pronotum slightly constricted anteriorly at collar, bearing dense, shallow punctures that are nearly confluent. Mesoscutellum subcircular. Elytra with 10 shallowly punctured striae; sutural striole absent; interstices convex, each interstice with a densely and shallowly punctured stria; elytral shoulders prominent. Abdomen with pygidium (tergite VII) exposed. Ventral and lateral surface sparsely covered with shallow punctures. Legs with tibial spur formula 1-2-2; trochanters small, triangular. Legs approximately equal in length or forelegs not distinctly longer/robust than mid- and hindlegs; procoxae touching, procoxal cavities open laterally with visible dorsal cleft; protibiae with an outer apical spine (uncus) and dense setal patch at inner apical angle; femora lacking spine at inner margin. Tarsi with article 1 rather narrow, not distinctly expanded; pretarsal claws (ungues) divaricate with inner subbasal swelling or tooth.

Holotype:

Zigras 174, Myanmar: Kachin; Cretaceous: Early Cenomanian; in the private collection of Mr. James S. Zigras.

Etymology:

Specific epithet derived from the Latin *nudus*, meaning "bare, naked", and the Latin *cornu*, meaning "horn", referring to the absence of a spine on ventrite 2 (a feature possessed by *Zigras cornus*).

Comments:

This species shares the interocular pair of tubercles with *Z. cornus*, though differs in lacking a spine on the abdominal venter. It also possesses a shorter rostrum which is not so strongly angled ventrad.

*Scabridus* **gen. nov.**

Type species: *Scabridus zigrasi* [as presently designated].

Diagnosis:

This genus is differentiated from *Zigras* mostly by the rough sculpturing of the cuticle and narrower and longer rostrum. While the rostrum length is more similar to that in *Cretonanophyes* (Baissorhynchinae), it is more orthognathous in form, directed anteriorly and broadly curved. While the compound eyes are similarly enlarged in this genus as in *Zigras*, they are not quite so protruding.

Etymology:

From the Latin *scabridus* meaning "rough or rugged", referring to the rough sculpturing of the cuticle.

*Scabridus zigrasi* **sp. nov.**

(Fig. 8)

Description:

Total body length (excluding rostrum): ca. 2.0 mm; maximal width (along middle of elytral): ca. 1.0 mm; elytral length: ca. 1.1 mm. Integument appearing light brown. Scales absent, but dense covering of short setae along dorsal, lateral, and ventral surfaces of body. Head not constricted before eyes. Compound eyes large and bulging, situated at base of rostrum, but more on head. Rostrum approximately 1.3x as long as pronotum along middle, slightly widening towards apex, then abruptly widening at apical 1/4; 4-7 stout setae placed laterally from antennal insertion to apex; two parallel, opposing, longitudinal rows of setae between eyes dorsally on head; shallow antennal scrobe apparently present ventrally, extending from point of antennal insertion to just before anterior margin of eyes. Antennae inserted ventrally at middle of rostrum, composed of scape, pedicel, funicle (flagellum) of 6 articles, and club of 3 articles; scape long, slender, nearly reaching anterior margin of eye; pedicel and funicular articles slightly elongate; club loose, apical 3rd article subconical, annulated at middle and appearing subdivided. Pronotum slightly roughly textured, slightly constricted anteriorly at collar, bearing dense, shallow punctures.

Mesoscutellum transverse, elliptical, bearing a dense, white setal patch. Elytra with very weak striae; sutural striole absent; interstices not elevated, with scattered punctures; elytral shoulders prominent. Abdomen with pygidium (tergite VII) concealed. Ventral and lateral surface sparsely covered with shallow punctures. Legs with tibial spur formula 1-2-2; trochanters small, triangular. Legs approximately equal in length; procoxae touching, procoxal cavities open laterally with visible dorsal cleft; mesocoxae nearly touching; protibiae with an outer apical spine (uncus) and dense setal patch at inner apical angle; all femora inflated, lacking spine at inner margin. Tarsi with article 1 rather narrow, not distinctly expanded; article 5 elongated, as long as articles 1-4 combined; pretarsal claws (ungues) divaricate with inner subbasal swelling.

Holotype:

Zigras 1, Myanmar: Kachin; Cretaceous: Early Cenomanian; in the private collection of Mr. James S. Zigras.

Etymology:

The specific epithet is a patronym dedicated to Mr. James Zigras, who obtained all of the Burmese specimens herein and permitted their examination.

Comments:

This species can be distinguished by the distinct pair of longitudinal setal rows between the compound eyes.

*Scabridus asperum* **sp. nov.**

(Figs. 9-10)

Description:

Total body length (excluding rostrum): ca. 3.2 mm; maximal width (along middle of elytral): ca. 1.0 mm; elytral length: ca. 2.1 mm. Integument appearing dark brown to black. Scales absent, but dense covering of short setae along dorsal and lateral surfaces of body, ventral surface apparently with more sparse setae. Head not constricted before eyes. Compound eyes large and bulging, situated at base of rostrum, but more on head. Rostrum approximately as long as pronotum along middle, slender, subequal in width along length. Antennae inserted laterally at middle of rostrum, composed of scape, pedicel, funicle (flagellum) of 6 articles, and club of 3 articles; scape long, slender, reaching or slightly surpassing anterior margin of eye; pedicel and funicular articles slender and elongate; club loose, apical 3rd article conical, annulated at middle and appearing subdivided. Pronotum roughly textured, slightly constricted posteriorly, narrowing anteriorly towards collar, bearing dense punctures. Mesoscutellum subspherical. Elytra roughly textured, with densely punctured striae; sutural striole absent; interstices convex with scattered punctures; elytral shoulders prominent. Abdomen with pygidium (tergite VII) concealed. Ventral and lateral surface sparsely covered with punctures. Legs with tibial spur formula 2-2-2; trochanters small, triangular. Legs approximately equal in length; procoxae apparently touching; femora fairly narrow (not markedly enlarged), lacking spine at inner margin. Tarsi with article 1 rather narrow, not distinctly expanded; pretarsal claws (ungues) divaricate with large inner subbasal tooth.

Holotype:

AMNH #Bu_FB89, available for study through the Division of Invertebrate Zoology, American Museum of Natural History (AMNH), New York, USA.

Paratype:

AMNH #Bu_FB88, available for study through the Division of Invertebrate Zoology, American Museum of Natural History (AMNH), New York, USA.

Etymology:

The specific epithet comes from the Latin *asper* meaning "rough" or "uneven," referring to the rough, punctured texture of the integument.

Comments:

Although the surface of the darkened cuticle is difficult to visualize in this species, it does not possess any distinct interocular setal patterning on the head, though shares a similar rough cuticular texture with *S. zigrasi*.

**Phylogeny of Caridae and related groups**:

*Morphology and characters*:

Morphological characters were derived from full body dissections of the extant taxa. In total, 288 characters were scored for 66 taxa, 36 of which were exemplar outgroup taxa from Nemonychidae, Anthribidae, Belidae, Attelabidae, Ithyceridae, Brentidae, Dryophthoridae, Erirhinidae, Brachyceridae, and Curculionidae, and 30 of which were carid taxa (20 genera).

*Taxon composition of Caridae*:

While sorting through the composition of the carids, it is important to reiterate the characters that give definition to this clade, particularly when presented with and trying to understand the fairly large quantity of fossil taxa, both described and undescribed (also see Davis et al. (2013) for more discussion regarding characters and previous confusion with Eccoptarthridae, Caridae, etc.). Groups such as *Eccoptarthroides* Legalov (2010), *Eccoptarthrus* Arnoldi (1977), *Ampliceps* Arnoldi (1977), etc., superficially resemble Caridae in occasionally possessing inflated femora and enlarged tarsomeres; however, as demonstrated in the phylogeny, such features are not unique to carids and present themselves in Nemonychidae and Belidae as well (Gratshev and Zherikhin 2000b; Kuschel 1983, 1994; Kuschel and Leschen 2011).

Following further examination, *Eccoptarthroides martynovi* Legalov (2010), although perhaps superficially appearing similar to *Cretonanophyes*, actually is a nemonychid which possesses a distinct labrum (Fig. 11) and probably is more related to the eobeline lineage.

The Baltic amber species *Baltocar succinicus* (Voss, 1953), placed in Caridae by Kuschel (1992), was transferred to Sayrevilleinae (Attelabidae) by Riedel *et al.* (2012). While this specimen does bear a carid gestalt, it has been found to assume a basal position within Attelabidae.

*Montsecanomalus zherikhini* Soriano *et al*. (2006) was described in the anomalous group Eccoptarthridae, now recognized as a group unrelated to Caridae, comprised of extinct nemonychids (albeit a still loosely-defined grouping) following the re-evaluation of the type genus and species, *Eccoptarthrus crassipes* Arnol'di, 1977 (Davis *et al*., 2013). After reviewing the information presented for *M. zherikhini*, it appears to be a true member of the eccoptarthrid group, similar to *Eccoptarthrus* Arnol'di (1977) and *Abrocar* Liu and Ren (2006). It is unclear whether the labrum actually is visible in the fossil, as it is quite rare to observe a distinct labrum in such compression fossils. Nonetheless, it is quite unfathomable why it would seem proper to place a taxon bearing a marked labrum together with the Caridae, a lineage far-removed from those which retain a separate labrum. The approximate medial insertion of the antennae on the rostrum and the short scape appear to be the only visible features grouping *M. zherikhini* with the other "eccoptarthrid" taxa (within Nemonychidae).

*Mongolocar orcinus* Gratshev et. Legalov (2011) also belongs to Nemonychidae, bearing a distinct labrum and apically inserted antennae composed of a short scape (Fig. 12).

While Legalov (2012) included *Nanophydes* Arnoldi (1977) in Carinae, at least its rostrum orientation and position on the head, as well as the apparent short scape and its position on the rostrum, indicate that is most likely is not a member of Caridae and possibly more closely related to eobelines.

*Other taxa possibly belonging to Caridae*:

Although most fossil holotypes were obtained and re-examined (Figs. 14-21), since a few fossil holotypes were not observed in this work, their definitive placement in Caridae could not be ascertained. These taxa have been described in other weevil groups; however, in reviewing the descriptions and associated figures/illustrations, a possible placement within or closer to Caridae may be hypothesized.

*Preclarusbelus vanini* Santos, Mermudes, and Medina da Fonseca (2007), described from the Santana Formation of northeastern Brazil, also bears some resemblance to Caridae. Its antennae appear to be inserted basally, and although most of the antenna is obscured, the lack of distinctly punctured elytral striae may exclude it from Caridae. While it possibly belongs in

Belidae, though even this placement may be questionable due to the specimen's preservation and the unobservable nature of most features which would be informative, it is at least not a member of Caridae.

*Arariperhinus monnei* Santos, Mermudes, and Medina da Fonseca (2011), although placed within Anthonomini (Curculionidae: Curculioninae), may possibly be a member of Caridae. While the authors discuss a rather certain placement in Curculioninae, the characters by which this definitive placement was made are not considered sufficient, namely a strongly convex body, slender rostrum, rounded eyes, and apparent lack of a prosternal sulcus (whichever one this may represent) and tibial spurs (despite the unobservable states of these last two characters). However, suggesting a definitive placement within Caridae based on critical features which are unobservable would only continue such unsupported speculation. Therefore, a possible placement of *A. monnei* within Caridae may only be suggested here based on the placement of the eyes on the base of the rostrum (as opposed to situated more on the cranium), an antennal insertion which appears more basal (as opposed to the stated apical insertion), and distinctly punctured elytral striae.

*Gratshevbelus erici* Soriano (2009) was described as a member of Eobelinae (presumably following the ideas of Arnol'di *et al*., 1977, in which this group was included within or near Belidae). Despite this placement, there are a number of inconsistencies which obscure such a strict assignment and provide a more carid-like impression. Such features include the large, convex eyes which appear to be positioned at the base of the rostrum, antennae which, although described as being inserted at the apical third of the rostrum, appear to be inserted at the basal one-third and also seem to have an elongate scape, the large, round pro- and mesocoxae, inflated, clavate femora, distinctly punctured elytral striae, and more rounded, convex body shape. While such features certainly allude to a possible placement close to Caridae, this supposition cannot be confirmed at this time.

In addition to the above taxa, several Mesozoic taxa have been described in Caridae which simply are too poorly-preserved to be associated to most weevil groups, particularly to this family and any subdivision therein (Legalov 2011). These taxa are *Karacar contractus* Gratshev et. Legalov (2011; Fig. 13), *Praecar stolidus* Gratshev et. Legalov (2011), *Mongolobrenthorrhinus* Gratshev et. Legalov 2011 (Legalov 2011), and *Testudobrenthorrhinus* Gratshev et. Legalov 2011 (Legalov 2011). While it is of great desire to classify fossil taxa with precision, such actions are on occasion unwarranted due to the rarity of verifiable characters. It may be possible to assign a certain gestalt to a fossil which lacks distinct characters due to its preservation; however, an attempt to accurately place such taxa in a phylogenetic analysis usually is not so facile and in many cases may be unachievable.

*Phylogeny*:

Construction of the character matrix was accomplished in Mesquite and analysis of the matrix was conducted in Nona (Goloboff 1999) through the interface of WinClada (Nixon 1999a) using parsimony as implemented by the ratchet function (Nixon 1999b). Analyses resulted in 704 most-parsimonious trees of length 1337. The 50% majority rules tree (Fig. 25) was of length 1337, with Ci=31 and Ri=65. The strict consensus tree (Fig. 26) was of length 1366, with Ci=30 and Ri=64.

*Relationships*:

Aside from its delineation, the placement of Caridae has been problematic. Zherikhin and Gratshev (1995) placed the group within Belidae, Kuschel (1992) and others regarded it as nested within Brentidae due to its likeness to Apioninae and Nanophyinae, Legalov (2009, 2010a, 2010b, 2012) included the group within Ithyceridae (among other groups), and Thompson (1992) and Zimmerman (1994) elevated it to a family. Indeed, while the taxa that comprise Caridae (see below checklist) all have superficial affinities to these other families, examination of more character systems was needed to more fully understand relationships and the distributions of characters.

While there has been much debate regarding sister group relationships of Caridae, as has been a general case within Curculionoidea, great problems exist in linking fossil forms with the extant fauna. As a result of recent fossil studies, as well as after reviewing older studies and examining undescribed material and described type material, it has become apparent that Caridae was a larger lineage with greater historical diversity (Figs. 25-26). Although the focus of this study resided more in exploring taxonomic relationships within the family and did not entirely encompass determining the classificatory placement of Caridae within Curculionoidea, it was of strong desire to provide better definition to the taxa that comprise this lineage, and in doing so determining its synapomorphic features. Consequently, a few things may be posited with regards to sister group relationships of Caridae. As Oberprieler *et al.* (2007) and others have noted before, Caridae is seen as a somewhat transitional group between primitive weevil families and the more derived and largest family, Curculionidae, both in life history characteristics and morphology. As a result of this study, an emphasis can be made on the degree of intermediate morphological features this family exhibits with respect to neighboring clades. It is through examples such as the Caridae in which it is possible to understand the complexity of the mixture of character states by which clades are defined morphologically.

In accordance with various previous morphological and molecular studies (Marvaldi and Morrone 2000, Marvaldi *et al.* 2002, McKenna *et al.* 2009, Oberprieler *et al.* 2007), Caridae appear sister with Ithyceridae or with Brentidae if including the former as subsumed in Brentidae. While Caridae and Ithyceridae + Brentidae appear as sister, they do not appear reciprocally monophyletic, as at least Brachyceridae, Erirhinidae, Dryophthoridae, and Curculionidae appear to belong to that more inclusive clade. Although Brentidae appears paraphyletic in this analysis, this result is thought to be more an artifact of taxon sampling. As the incorporation of numerous fossil taxa does not permit extraction of complete character datasets, this point is illustrated well by the results portrayed in the strict consensus tree (Fig. 26). As such, a 50% majority rules tree also is presented which may provide a more complete depiction of the relationships within the family (Fig. 25). The groups comprising Carinae and Baissorhynchinae appear to have substantial character congruence and support, leaving a basal grade of fossil groups. Mesophyletinae is composed of just two genera which seem to form a cohesive group. It is possible that the adjacent genera, such as *Zigras*, *Scabridus*, and a few undescribed taxa (identified here as Caridae 1, 2, 3; Figs. 22, 23, and 24, respectively) would be included within Mesophyletinae as well due to their affinities in tarsi and pretarsal claw structure and antennal scape length. Therefore, their separation in the phylogenetic analysis could be a product of the limited information available as fossil forms.

**Classification of Caridae**:

Classification and checklist of Caridae as delineated by this study (†=exinct taxon):

Caridae Thompson, 1992 (Type genus: *Car* Blackburn, 1897)

**Carinae** Thompson, 1992

*Caenominurus* Voss, 1965 (Type species: *C. topali*)

*C. topali* Voss, 1965

*Car* Blackburn, 1897 (Type species: *C. condensatus*)

*C. condensatus* Blackburn, 1897

*C. intermedius* Lea, 1926

*Carodes* Zimmerman, 1994 (Type species: *C. revelatus*)

*C. revelatus* Zimmerman, 1994

*Chilecar* Kuschel, 1992 (Type species: *C. pilgerodendri*)

*C. pilgerodendri* Kuschel, 1992

*Crowsonicar* Legalov, 2013 (Type species: *C. pini*)

*C. pini* (Lea, 1911)

†*Albicar* Peris, Davis, Engel et Delclòs, 2014 (Type species: *A. contriti*)

*A. contriti* Peris, Davis, Engel et Delclòs, 2014

†*Cretocar* Gratshev & Zherikhin, 2000b (Type species: *C. luzzii*)

*C. luzzii* Gratshev & Zherikhin, 2000b

†*Martinsnetoa* Zherikhin & Gratshev, 2004 (Type species: *M. dubia*)

*M. dubia* Zherikhin & Gratshev, 2004 (AMNH no. 43315; specimen lost?)

†J*arzembowskia* Zherikhin & Gratshev, 1997 (Type species: J. *edmundi*)

*J. edmundi* Zherikhin & Gratshev, 1997 (BM no. IN_49648)

†**Baissorhynchinae** Zherikhin, 1993

†*Baissorhynchus* Zherikhin, 1977 (Type species: *B. tarsalis*)

*B. tarsalis* Zherikhin, 1977

†*Emanrhynchus* Zherikhin, 1993 (Type species: *E. lebedevi*)

*E. lebedevi* Zherikhin, 1993

†*Gobicar* Gratshev & Zherikhin, 1999 (Type species: *G. ponomarenkoi*)

*G. ponomarenkoi* Gratshev & Zherikhin, 1999

*G. hispanicus* Gratshev & Zherikhin, 2000a

†*Cretonanophyes* Zherikhin, 1977 (Type species: *C. longirostris*)

=†*Hispanocar* Soriano *et al*., 2006 **n. syn.**

C. *edmundi* (Zherikhin & Gratshev, 1997) **n. comb.**

*C. kseniae* (Soriano *et al*., 2006) **n. comb.**

*C. longirostris* Zherikhin, 1977

*C. punctatus* Liu & Ren, 2007

*C. zherikhini* Liu & Ren, 2006

*C. rugosithorax* Gratshev & Zherikhin, 2000a

†**Mesophyletinae**

†*Anchineus* Poinar and Brown, 2009 (Type species: *A. dolichobothris*)

*A. dolichobothris* Poinar and Brown, 2009

†*Mesophyletis* Poinar, 2006 (Type species: *M. calhouni* [designated in Poinar 2008)

*M. calhouni* Poinar, 2006

***Incertae Sedis***

†*Scabridus* **gen. nov.** (Type species: *S. zigrasi*)

*S. asperum* **sp. nov.**

*S. zigrasi* **sp. nov.**

†*Zigras* **gen. nov.** (Type species: *Z. cornus*)

*Z. cornus* **sp. nov.**

*Z. nudicornus* **sp. nov.**

†*Baissacar* Gratshev et. Legalov, 2011 (Type species: *B. passarius*)

*B. passarius* Gratshev et. Legalov, 2011

†*Palaeocar* Gratshev et. Legalov, 2011 (Type species: *P. princeps*)

*P. princeps* Gratshev et. Legalov, 2011

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**Figure legends**:

**Figs. 1-3**. 1, *Car* sp. 1a, dorsal aspect; 1b, lateral aspect; 1c, metanotum. 2, *Caenominurus topali*. 2a, dorsal aspect; 2b, lateral aspect; 2c, metanotum. 3, *Chilecar pilgerodendri*. 3a, dorsal aspect; 3b, lateral aspect; 3c, metanotum.

**Fig. 4**. *Cretonanophyes punctatus* Liu & Ren. 4a, photomicrograph of specimen; 4b, enlargement of metanotal area of 4a; 4c, illustration of metanotal area.

**Fig. 5**. *Zigras cornus* **sp. nov.** (holotype). 5a, lateral aspect of specimen; 5b, illustration of lateral aspect; 5c, postero-ventral aspect, showing ventral spine; 5d, illustration of postero-ventral aspect.

**Fig. 6**. *Zigras cornus* **sp. nov.** (paratype). 6a, lateral aspect of specimen; 6b, illustration of lateral aspect; 6c, illustration of lateral aspect of head, revealing more of the rostrum and antennal scape.

**Fig. 7**. *Zigras nudicornus* **sp. nov.** 7a, lateral aspect of specimen; 7b, illustration of lateral aspect; 7c, lateral aspect of opposing side of specimen.

**Fig. 8**. *Scabridus zigrasi* **sp. nov.** 8a, dorsal aspect of specimen; 8b, illustration of dorsal aspect; 8c, illustration of posterior aspect, showing ovipositor; 8d, postero-ventral aspect of specimen;

8e, ventral aspect of specimen; 8f, illustration of part of postero-ventral aspect; 8g, illustration of hind tarsus.

**Fig. 9**. *Scabridus asperum* **sp. nov.** (holotype). 9a, dorsal aspect of specimen; 9b, illustration of dorsal aspect; 9c, lateral aspect of specimen.

**Fig. 10**. *Scabridus asperum* **sp. nov.** (paratype). 10a, posterior aspect of specimen; 10b, ventro-lateral aspect of specimen; 10c, illustration of ventro-lateral aspect; 10d, dorsal aspect of specimen; 10e, illustration of dorsal aspect; 10f, illustration of portion of hind tarsus.

**Fig. 11**. *Eccoptarthroides martynovi* Legalov (holotype). 11a, photomicrograph of specimen; 11b, illustration.

**Fig. 12**. *Mongolocar orcinus* Gratshev et. Legalov (holotype). 12a, photomicrograph of specimen; 12b, illustration.

**Fig. 13**. *Karacar contractus* Gratshev et. Legalov (holotype). 13a, photomicrograph of specimen; 13b, illustration.

**Fig. 14**. *Cretocar luzzii* Gratshev & Zherikhin (holotype). 14a, photomicrograph of specimen, lateral aspect; 14b, illustration.

**Fig. 15**. *Cretocar luzzii* Gratshev & Zherikhin (holotype). 15a, photomicrograph of specimen, lateral aspect (opposing side); 15b, illustration.

**Fig. 16**. J*arzembowskia edmundi* Zherikhin & Gratshev (holotype). 16a, photomicrograph of specimen; 16b, illustration.

**Fig. 17**. *Emanrhynchus lebedevi* Zherikhin (holotype). 17a, photomicrograph of specimen; 17b, illustration.

**Fig. 18**. *Gobicar ponomarenkoi* Gratshev & Zherikhin (holotype). 18a, photomicrograph of specimen; 18b, illustration.

**Fig. 19**. *Cretonanophyes* sp. (undescribed). 19a, photomicrograph of specimen; 19b, illustration.

**Fig. 20**. *Baissacar passarius* Gratshev et. Legalov (holotype). 20a, photomicrograph of specimen; 20b, illustration.

**Fig. 21**. *Palaeocar princeps* Gratshev et. Legalov (holotype). 21a, photomicrograph of specimen; 21b, illustration.

**Fig. 22**. Undescribed Caridae (Karatau). Caridae1. 22a, photomicrograph of part; 22b, photomicrograph of counterpart; 22c, illustration of counterpart.

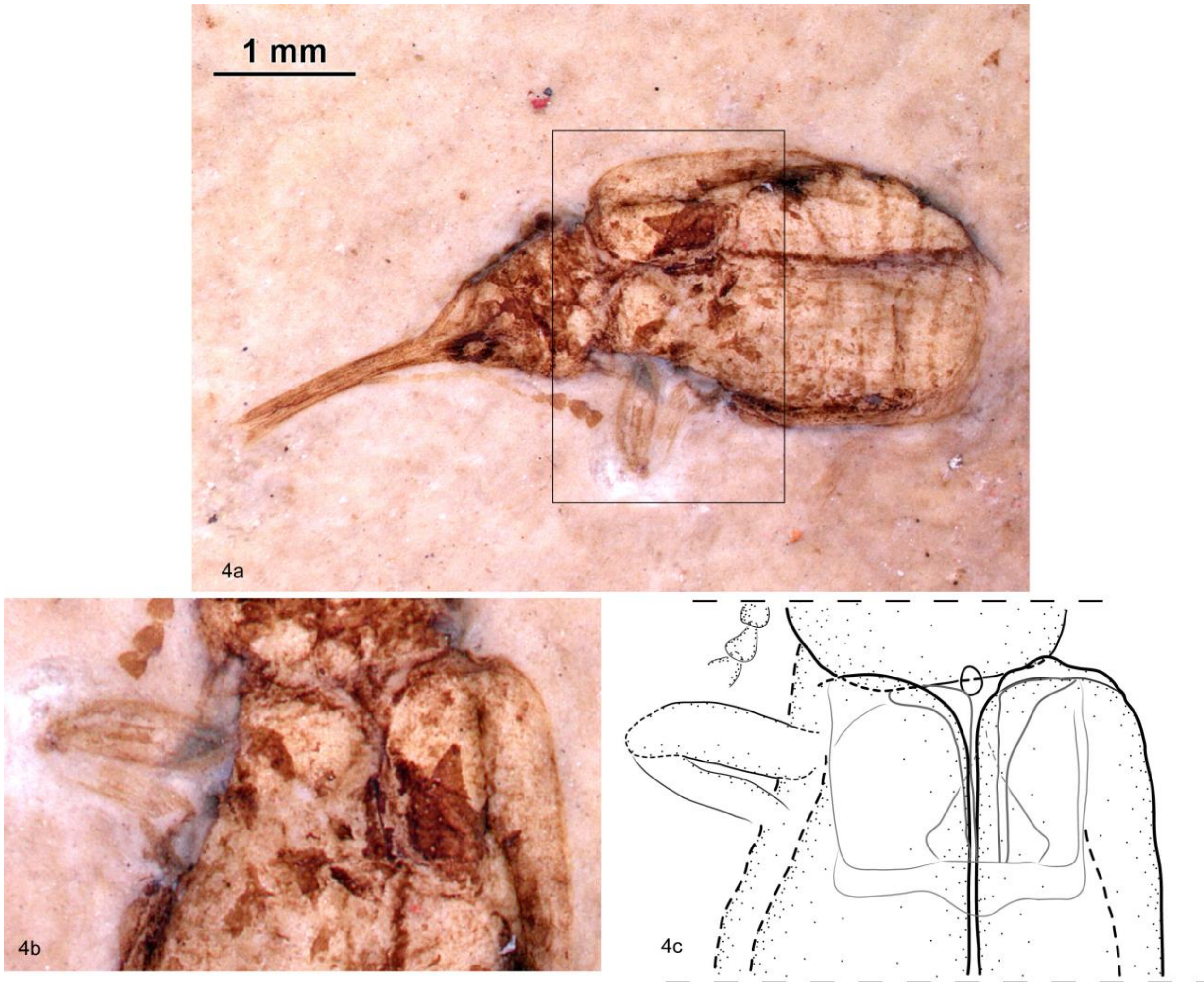
**Fig. 23**. Undescribed Caridae (Karatau). Caridae2. 23a, photomicrograph of specimen; 23b, illustration.

**Fig. 24**. Undescribed Caridae (Karatau). Caridae3. 24a, photomicrograph of part; 24b, illustration of part; 24c, enlargement of head, pro- and mesosternum of part; 24d, photomicrograph of counterpart.

**Fig. 25**. 50% majority rules tree (integers appearing at nodes represent the percentage in which a particular clade is present among all most-parsimonious trees obtained), L=1337, Ci=31, Ri=65.

**Fig. 26**. Strict consensus tree of 704 most-parsimonious trees, L=1366, Ci=30, Ri=64.


1a
1b
1c
2a
2b
2c
3a
3b
3c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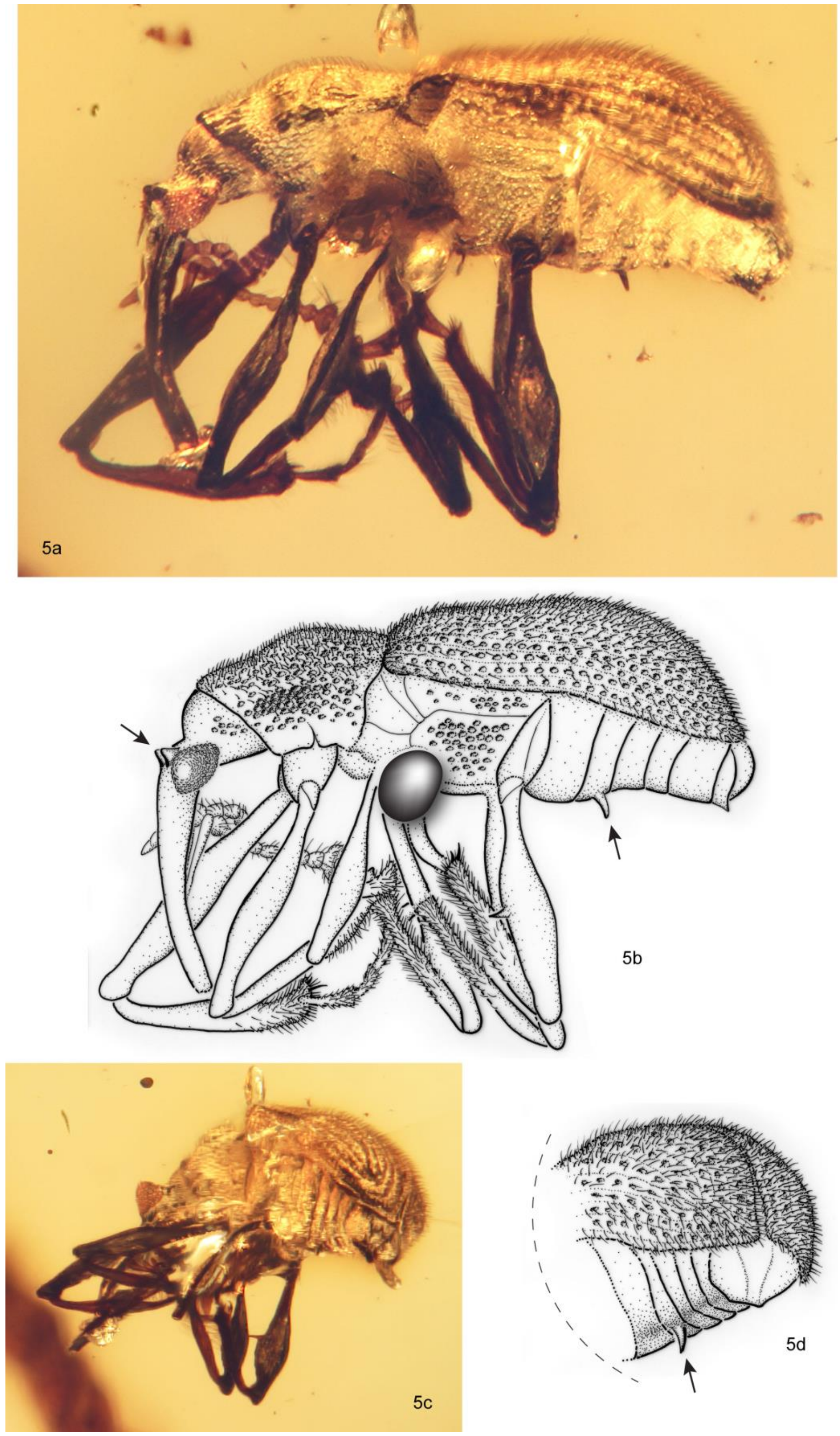
4a
4b
4c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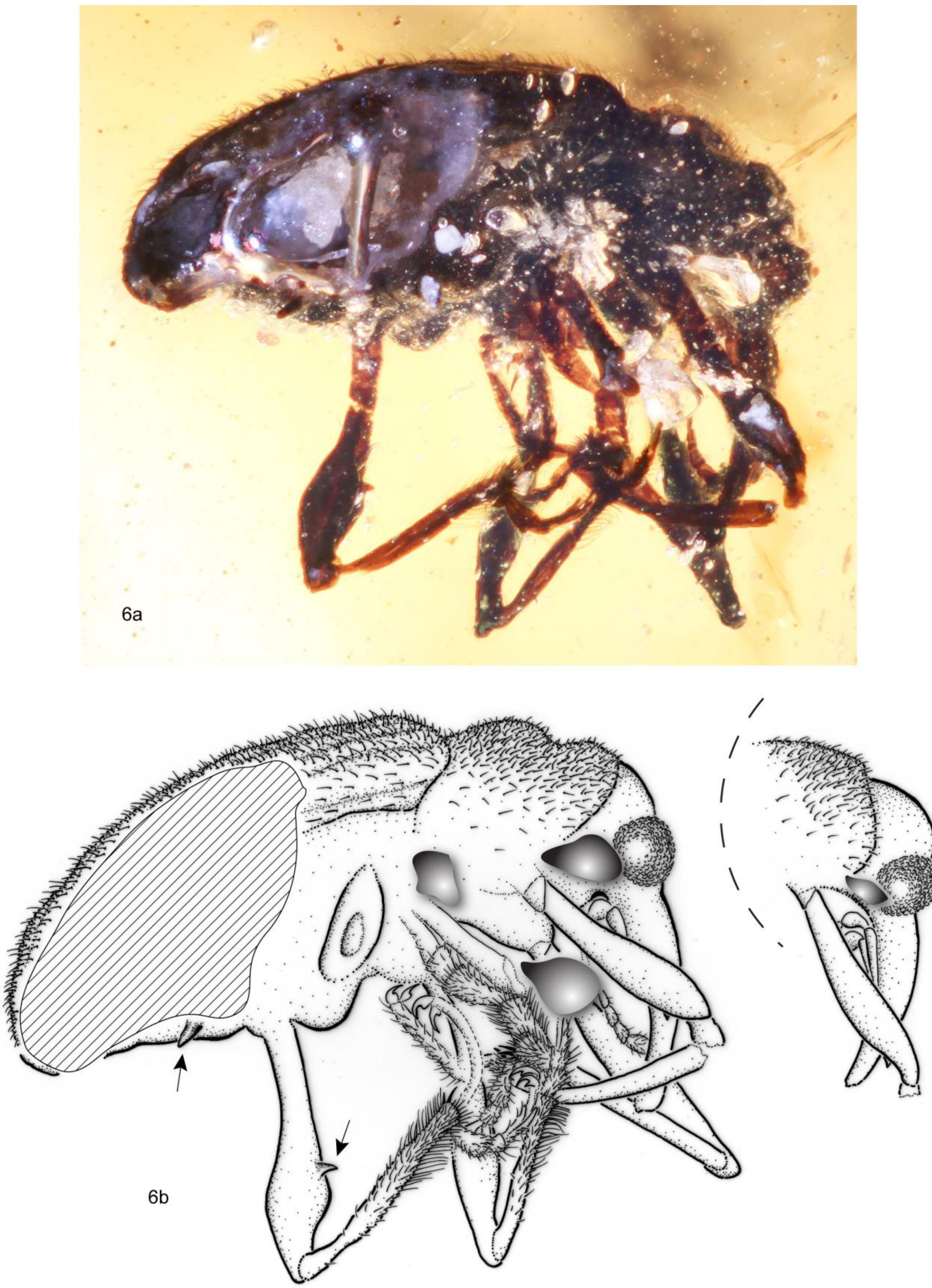
5d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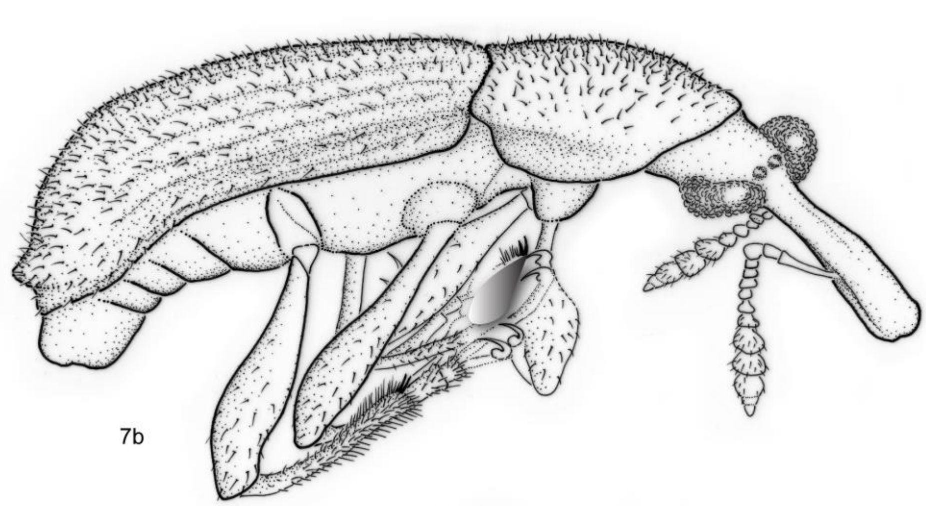
7a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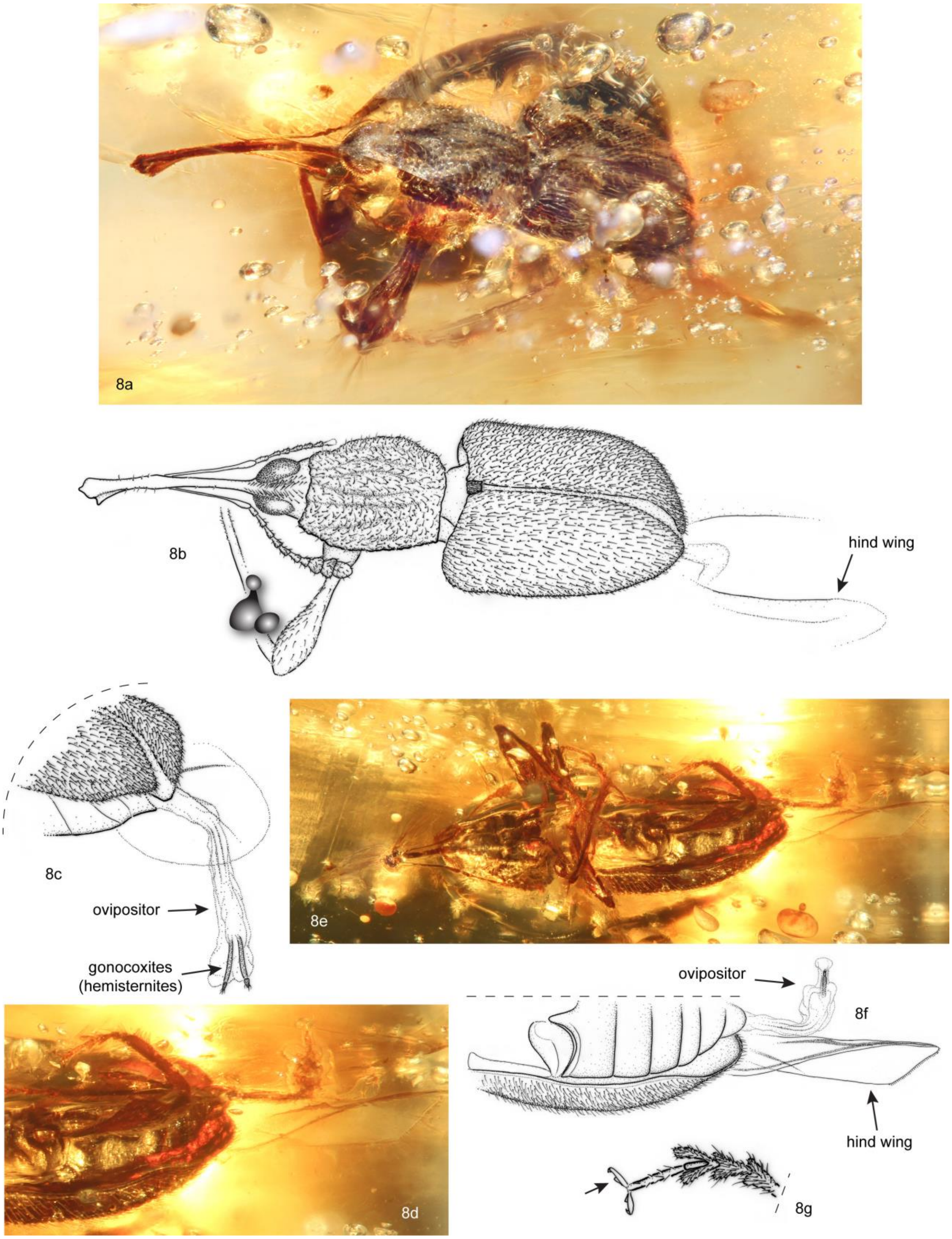
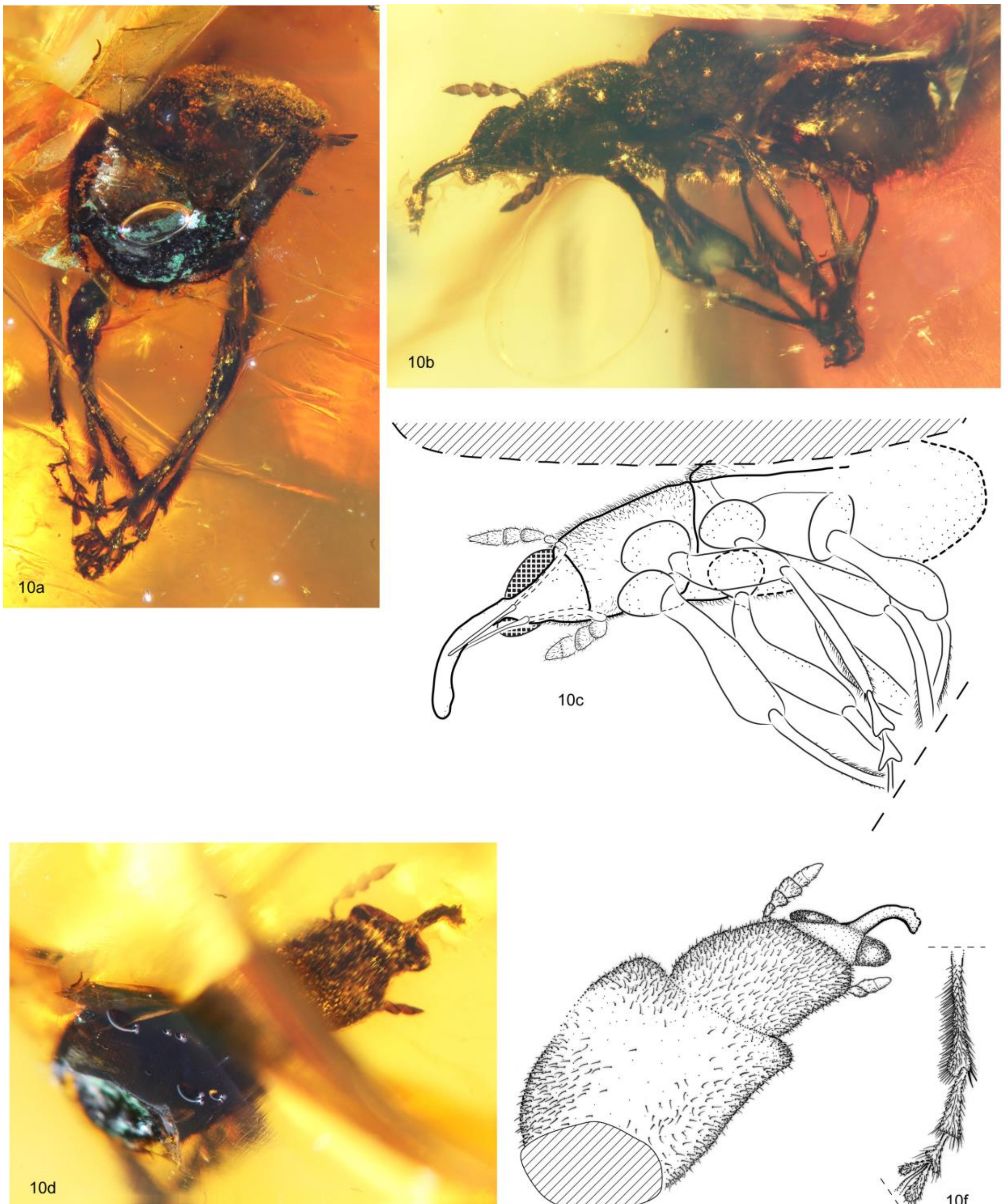
7c


8a
8b
hind wing
8c
ovipositor
gonocoxites
(hemisternites)
8e
ovipositor
8f
hind wing
8g
8d


9a
9b
9c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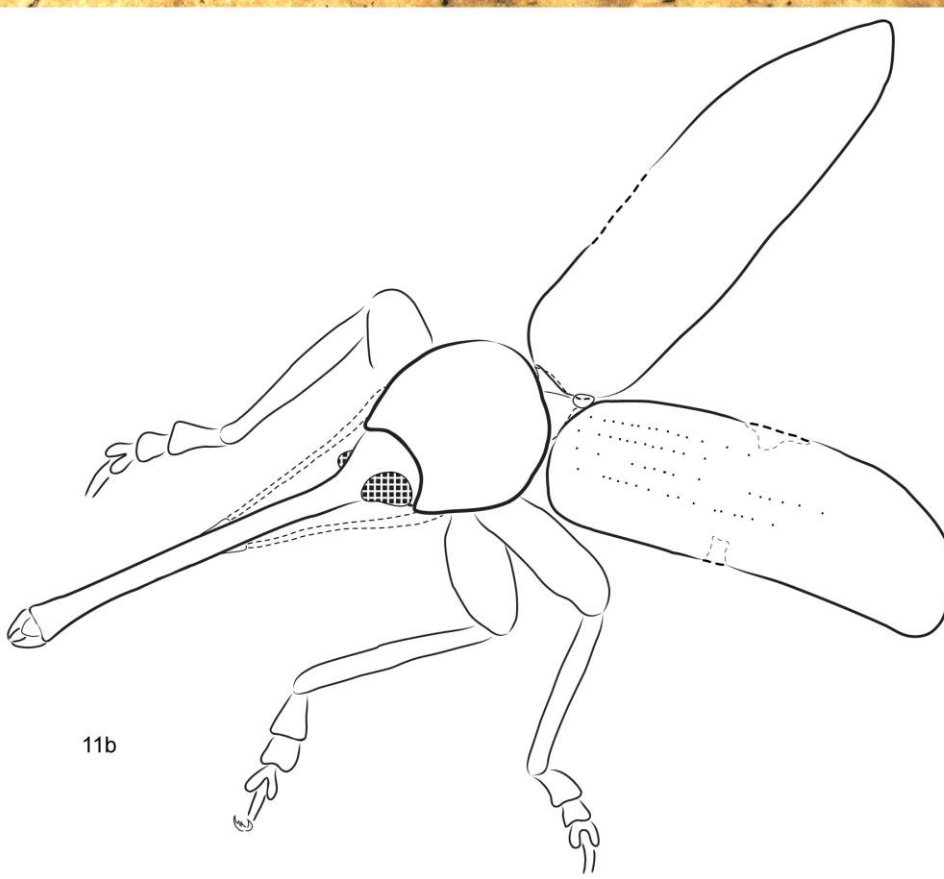
10c
10d
10e
10f


0,50 mm
11a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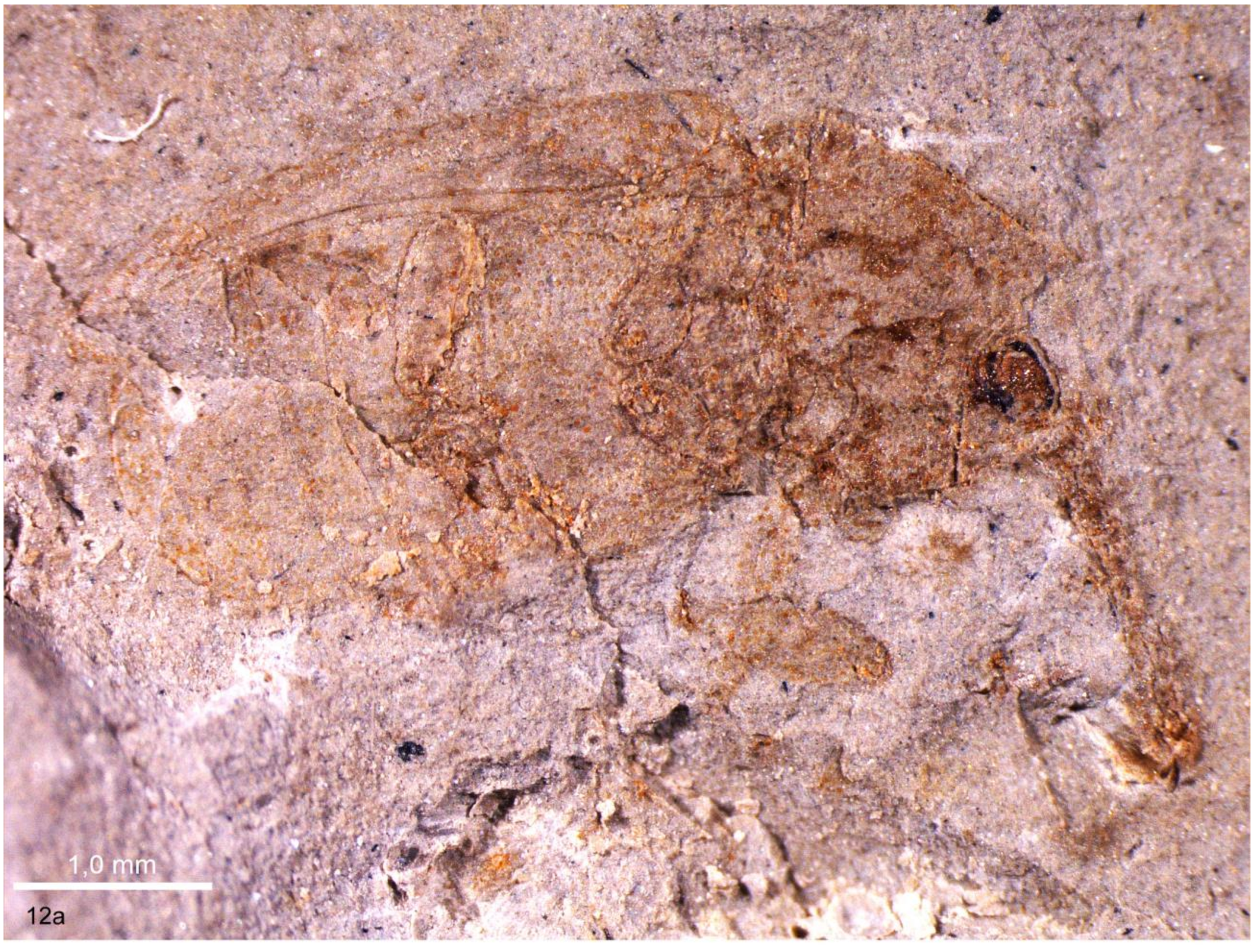


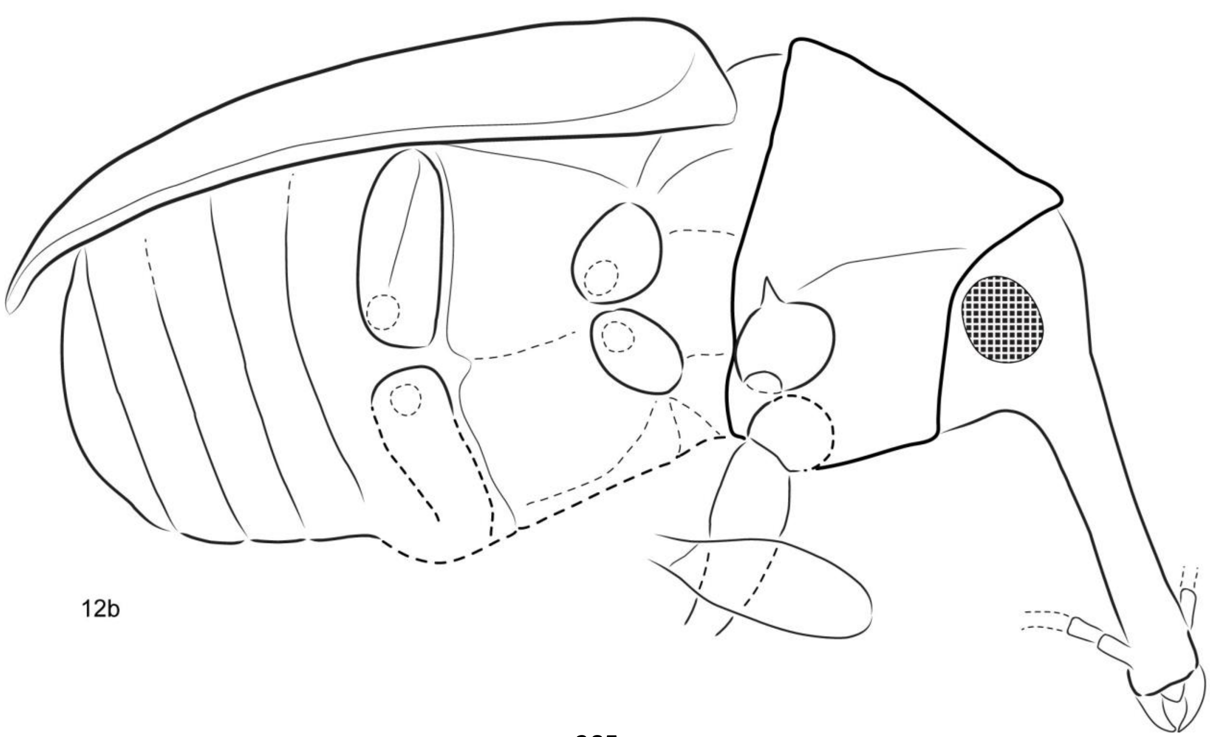

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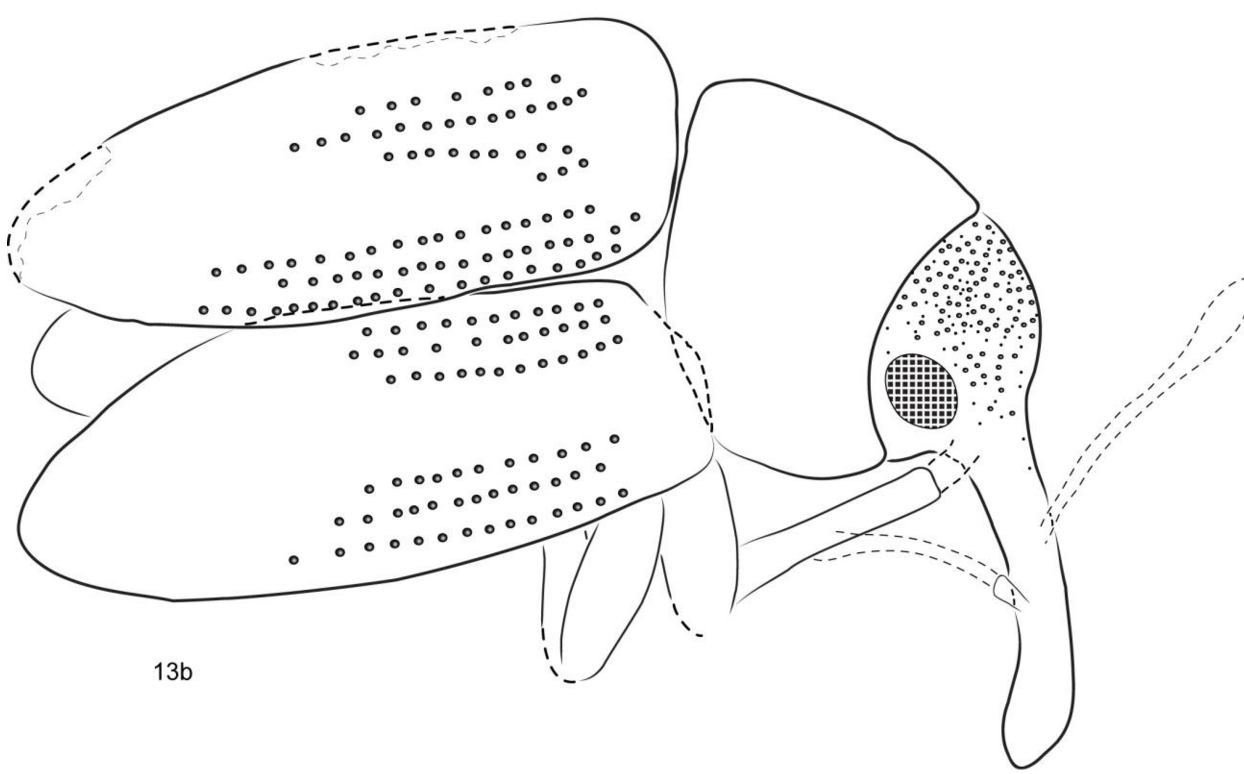
13a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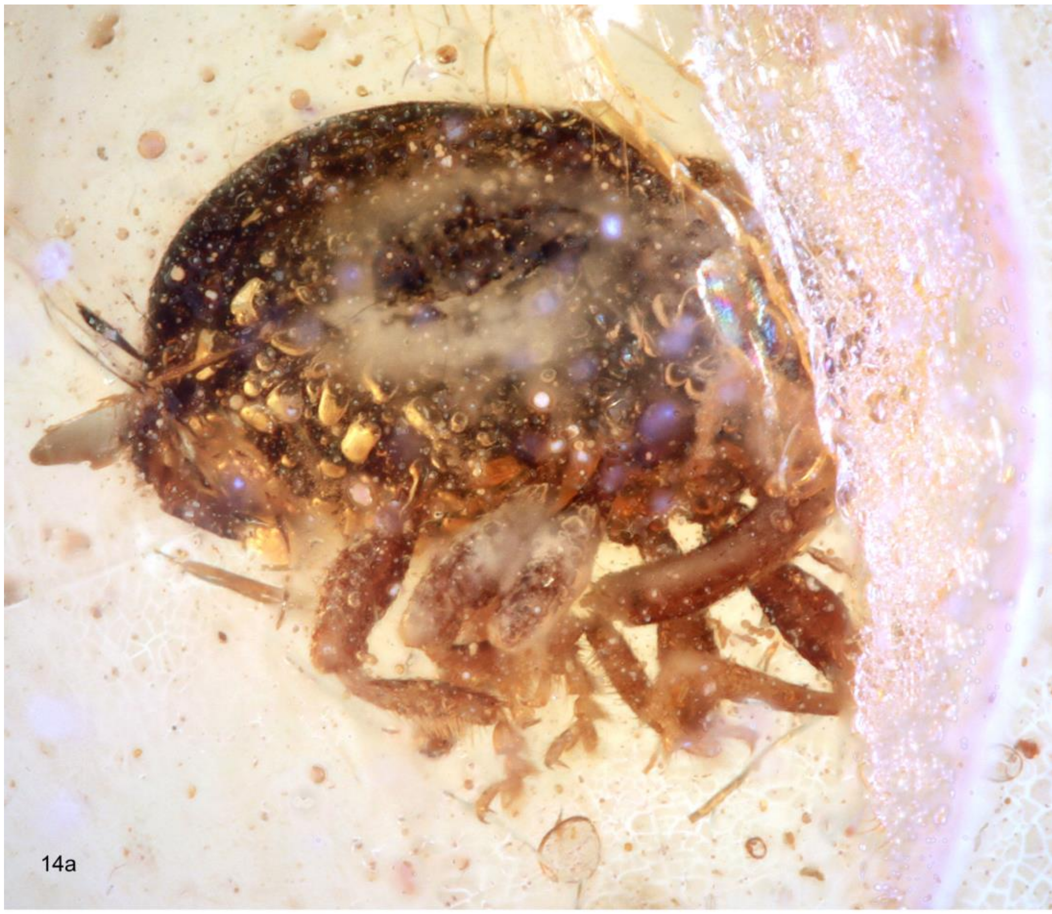

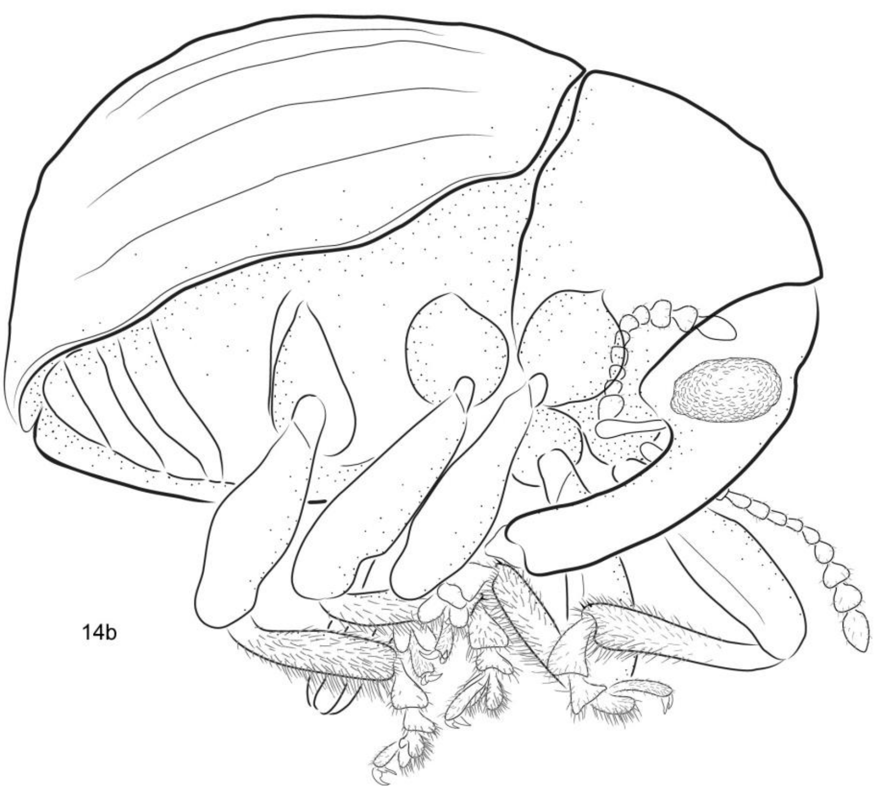


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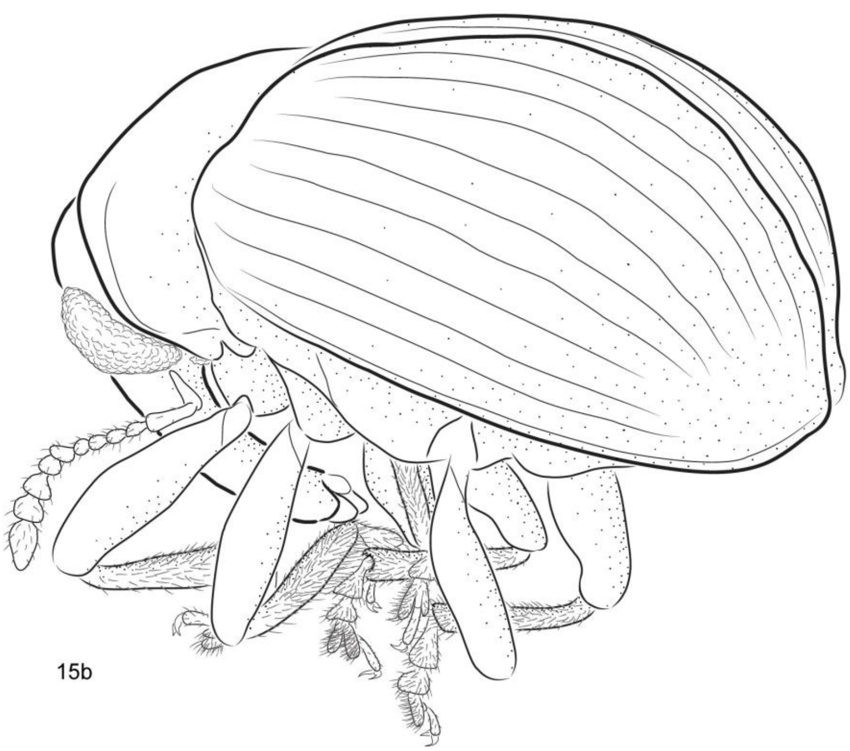
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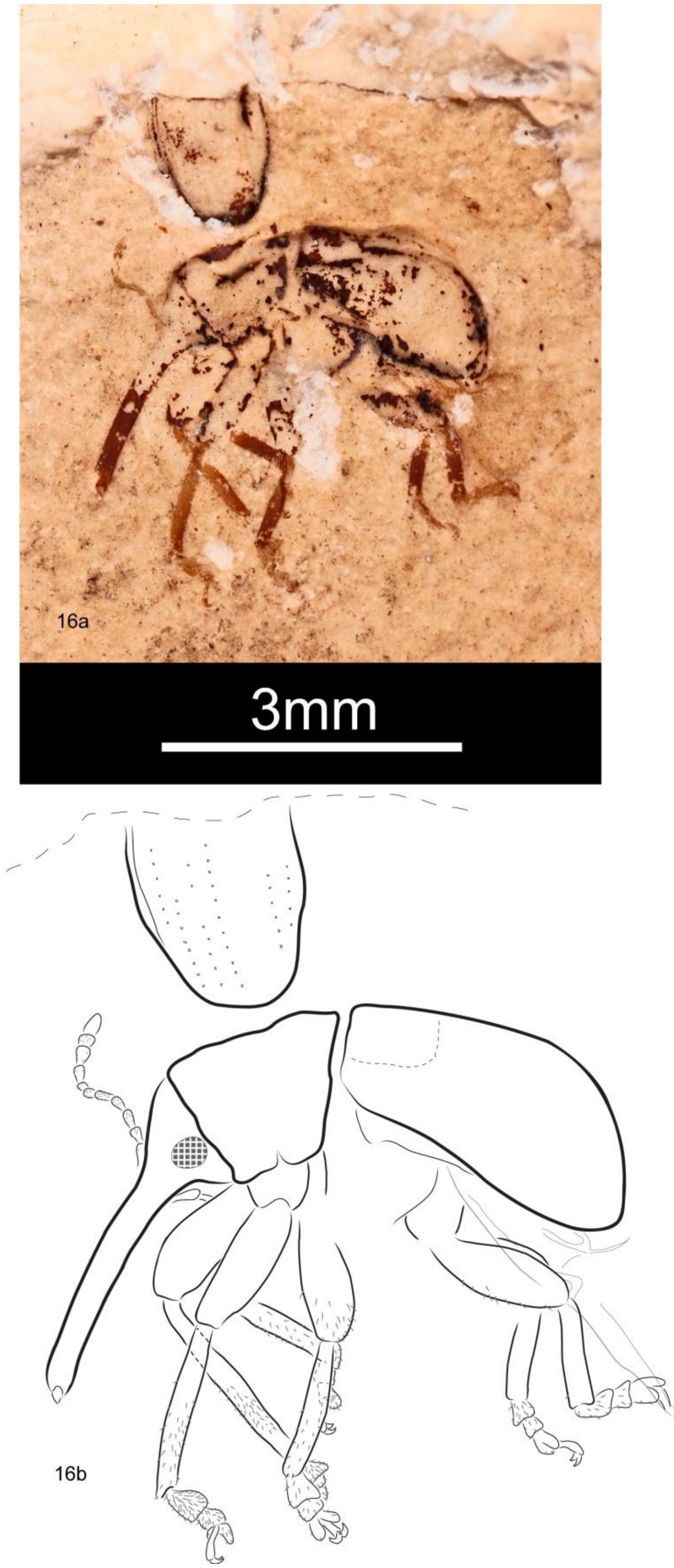
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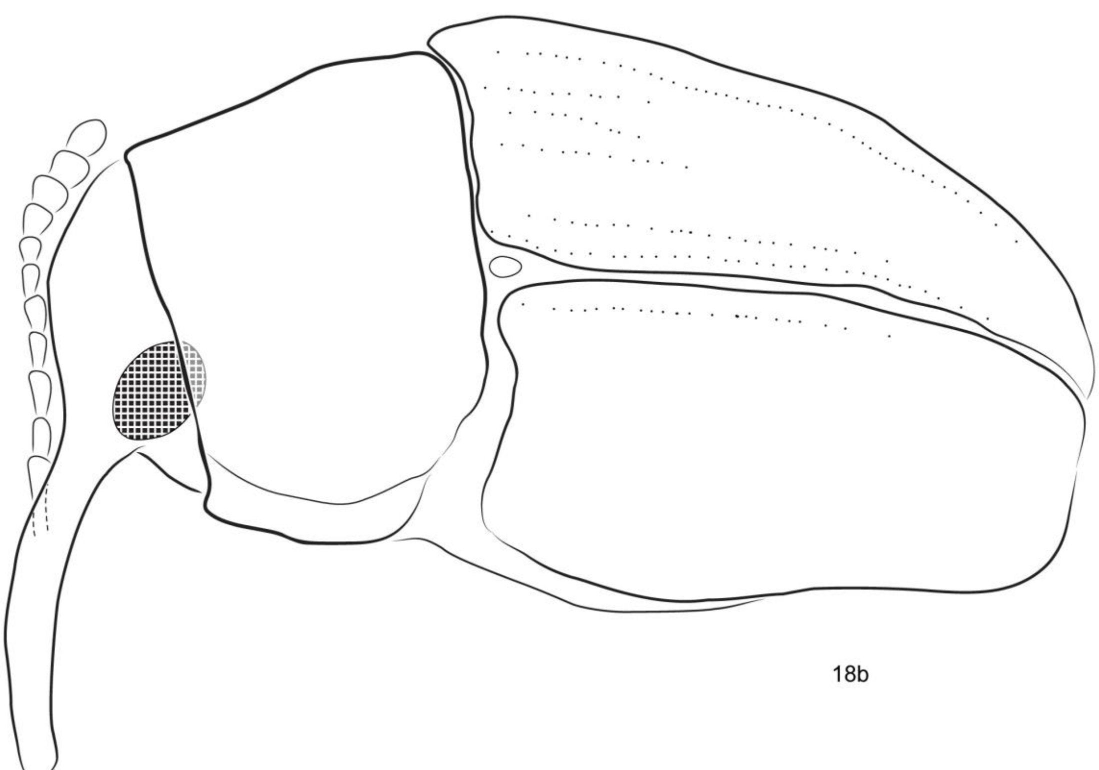
3mm
16b


1,0 mm
17a
17b

18a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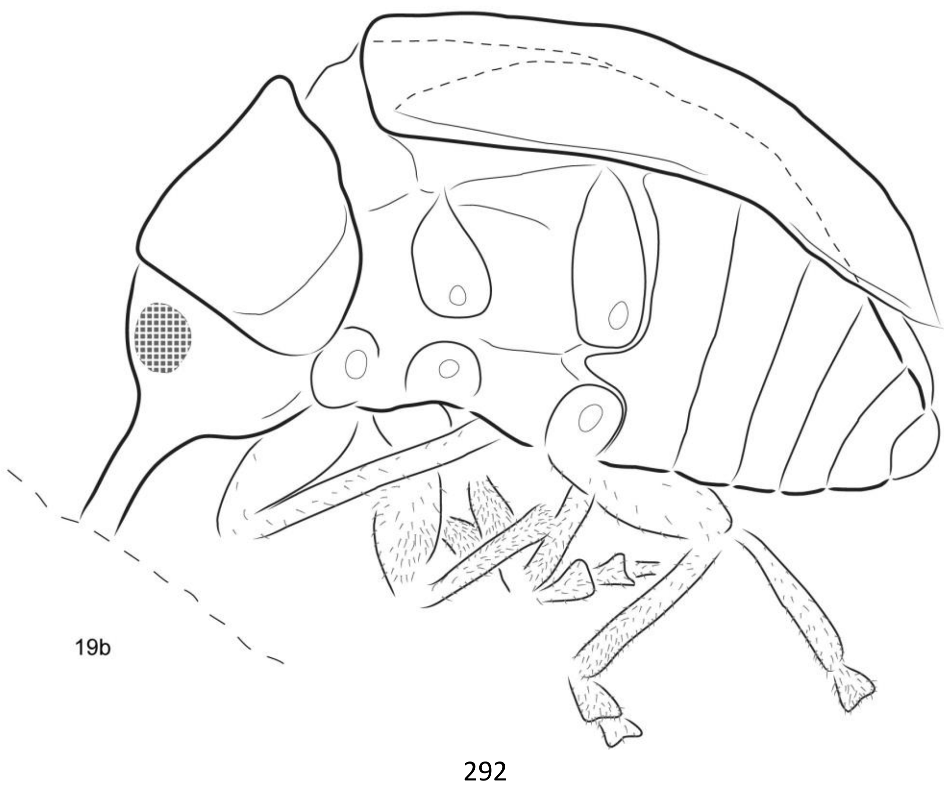
19a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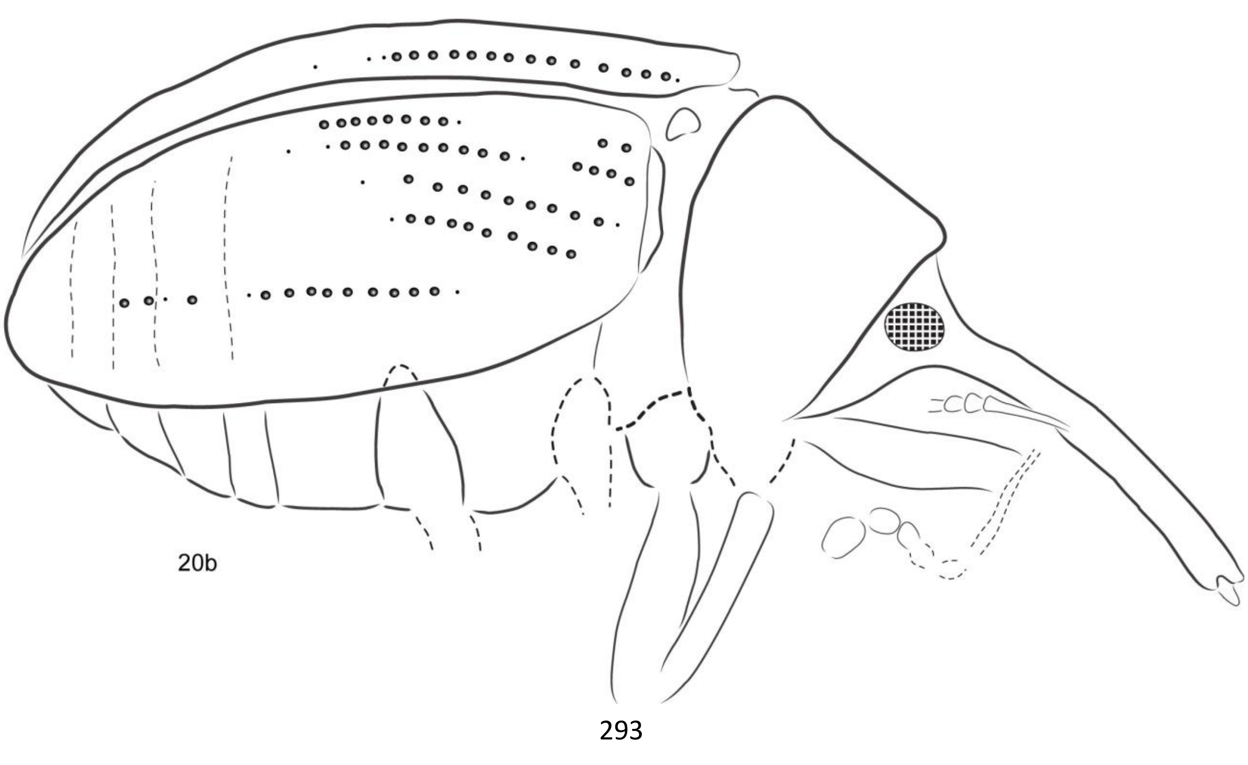

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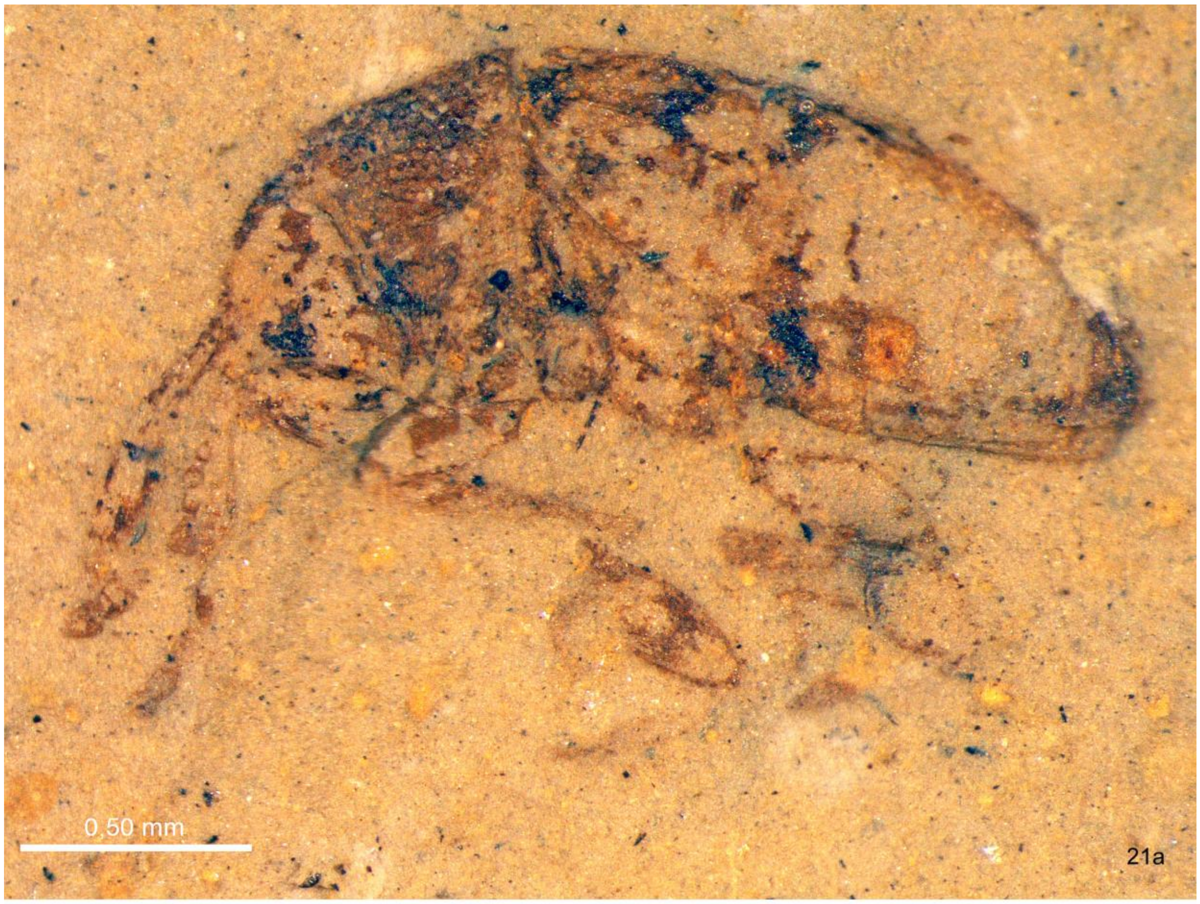
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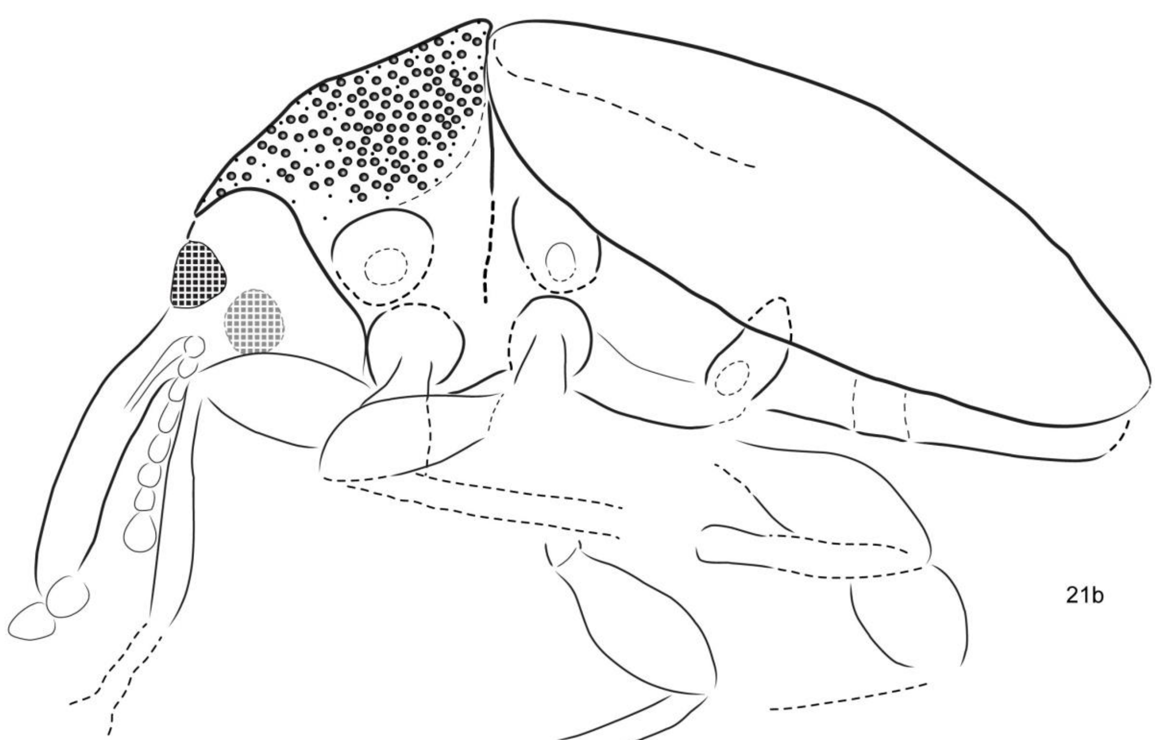
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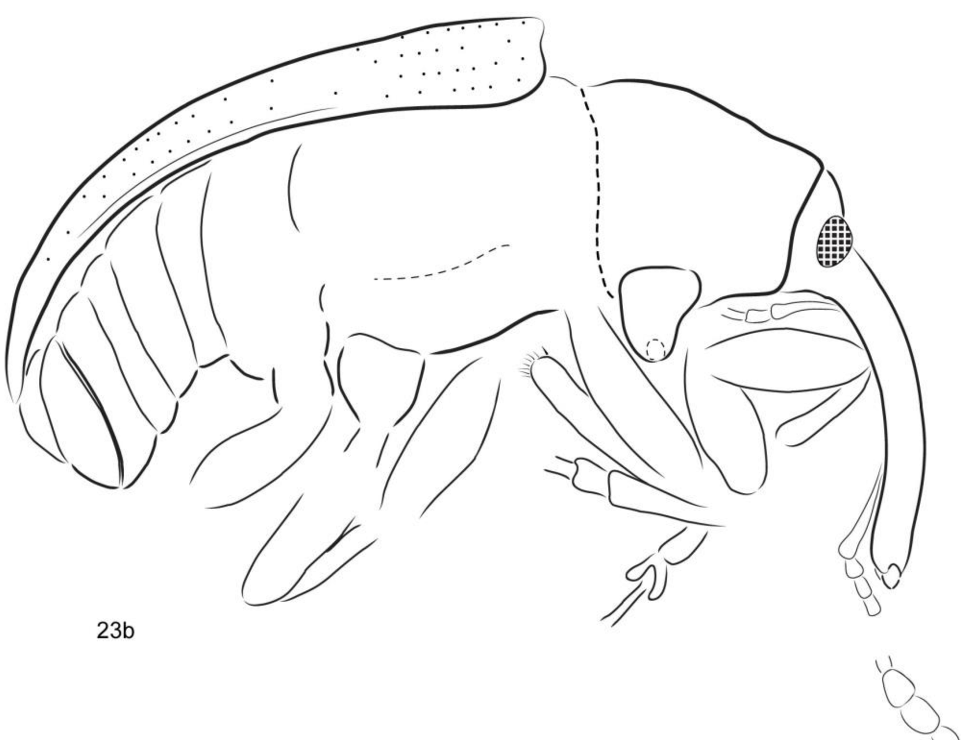
0,50 mm
22a
0,50 mm
22b
22c

23b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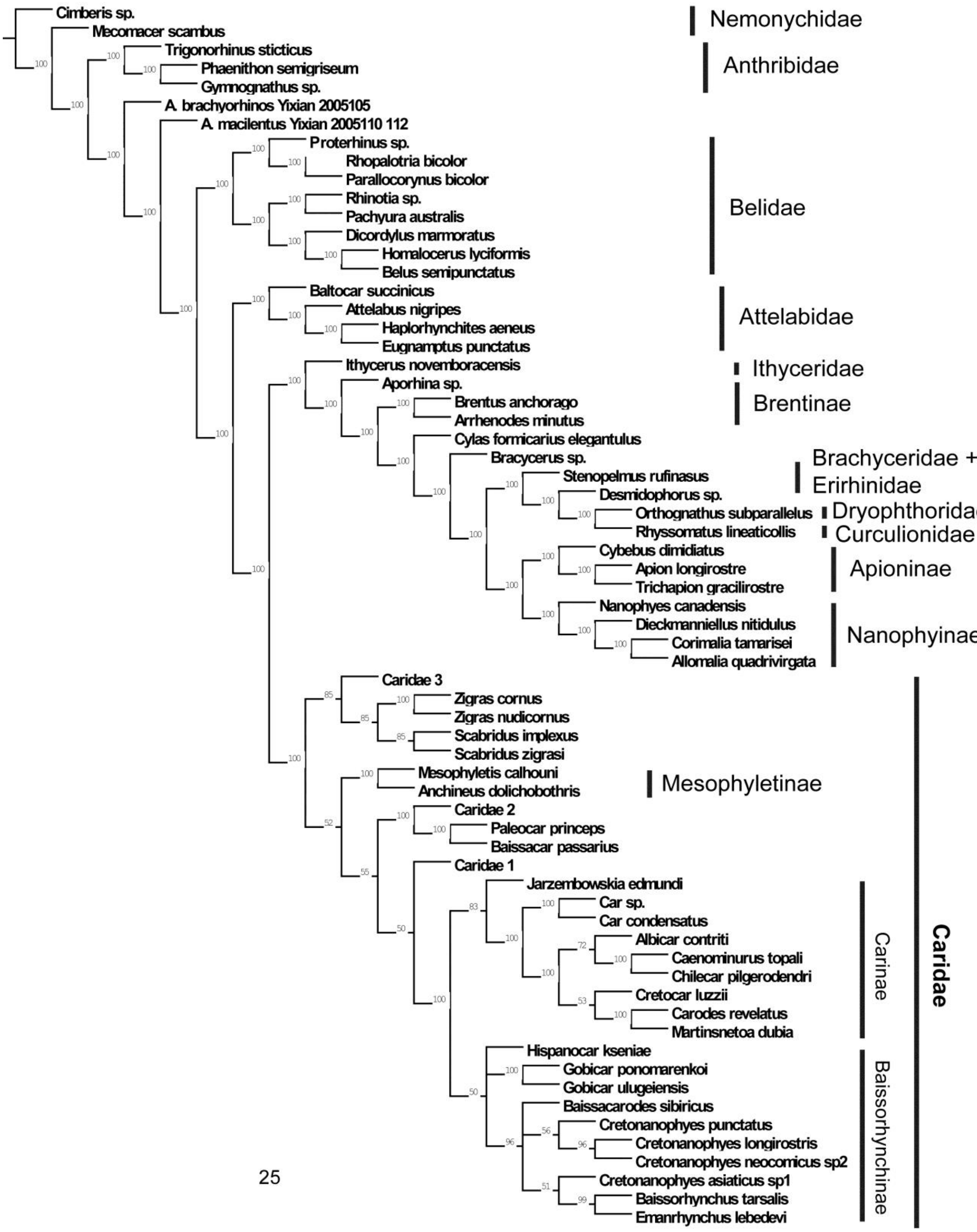
24d



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A. brachyorhinos Yixian 2005105
A. macilentus Yixian 2005110 112
Proterhinus sp.
Rhopalotria bicolor
Parallocorynus bicolor
Rhinotia sp.
Pachyura australis
Dicordylus marmoratus
Homalocerus lyciformis
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Attelabus nigripes
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Desmidophorus sp.
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Trichapion gracilirostre
Nanophyes canadensis
Dieckmanniellus nitidulus
Corimalia tamarisei
Allomalia quadrivirgata
Caridae 3
Zigras cornus
Zigras nudicornus
Scabridus implexus
Scabridus zigrasi
Mesophyletis calhouni
Anchineus dolichobothris
Caridae 2
Paleocar princeps
Baissacar passarius
Caridae 1
Jarzembowskia edmundi
Car sp.
Car condensatus
Albicar contriti
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Cretocar luzzii
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Martinsnetoa dubia
Hispanocar kseniae
Gobicar ponomarenkoi
Gobicar ulugeiensis
Baissacarodes sibiricus
Cretonanophyes punctatus
Cretonanophyes longirostris
Cretonanophyes neocomicus sp2
Cretonanophyes asiaticus sp1
Baissorhynchus tarsalis
Emanrhynchus lebedevi
Nemonychidae
Anthribidae
Belidae
Attelabidae
Ithyceridae
Brentinae
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Caridae
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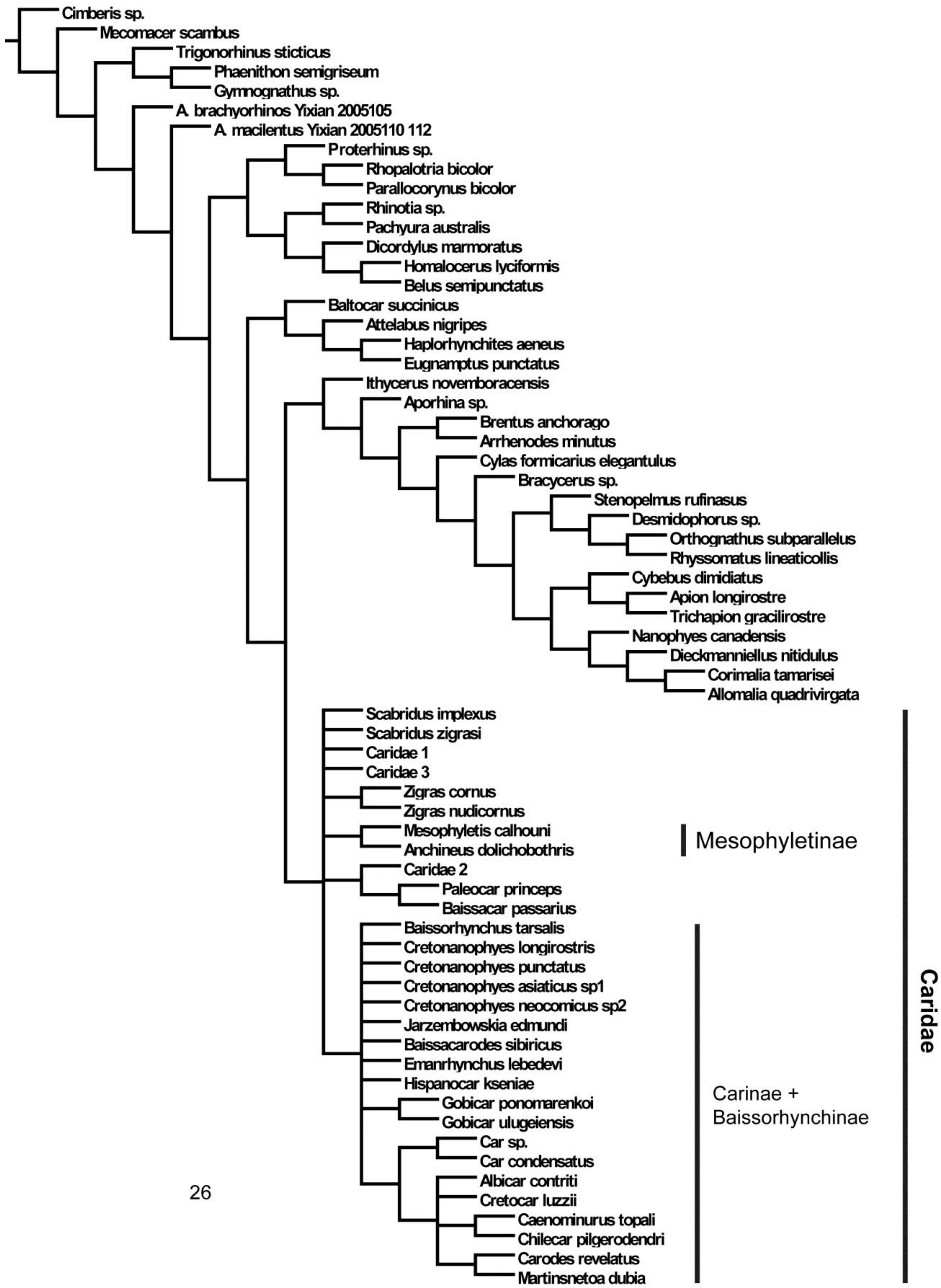
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A. macilentus Yixian 2005110 112
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Trichapion gracilirostre
Nanophyes canadensis
Dieckmanniellus nitidulus
Corimalia tamarisei
Allomalia quadrivirgata
Scabridus implexus
Scabridus zigrasi
Caridae 1
Caridae 3
Zigras cornus
Zigras nudicornus
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Anchineus dolichobothris
Mesophyletinae
Caridae 2
Paleocar princeps
Baissacar passarius
Baissorhynchus tarsalis
Cretonanophyes longirostris
Cretonanophyes punctatus
Cretonanophyes asiaticus sp1
Cretonanophyes neocomicus sp2
Jarzembowskia edmundi
Baissacarodes sibiricus
Emanrhynchus lebedevi
Hispanocar kseniae
Gobicar ponomarenkoi
Gobicar ulugeiensis
Car sp.
Car condensatus
Albicar contriti
Cretocar luzzii
Caenominurus topali
Chilecar pilgerodendri
Carodes revelatus
Martinsnetoa dubia
Carinae +
Baissorhynchinae
Caridae

# 4. Rostrum structure and development in the rice weevil *Sitophilus oryzae* (Coleoptera: Curculionidae)

**Davis, Steven R.**

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email: steved@ku.edu

## Abstract

A documentation and review of weevil rostrum growth is made through examination of the developmental life stages in the rice weevil *Sitophilus oryzae* (Linnaeus). Histological and morphological examinations are made utilizing light, fluorescent, and electron microscopy. In *S. oryzae*, rostral tissue begins proliferating in the late 4$^{th}$ instar larva and continuing through to the pupal stage, with the majority of rostrum growth taking place in the prepupa. Adult cranial and rostral morphology is also reviewed, focusing on structures that may be pertinent to phylogeny reconstruction. The weevil rostrum is essentially an extension of various head sclerites that are basal to the mouthparts. Therefore, while the mouthparts are fairly similar to other Coleoptera in basic form, the head is markedly different due to its anterior extension. By understanding the more noticeable details of rostrum growth and structure, this study may serve as a foundation for comparative studies of a similar nature and as a basis for beginning research on the genetic nature of rostrum formation and evolution throughout the weevil clade.

## 1. Introduction

The study of developmental mechanisms, including appendage formation, in insects has been relatively limited to model organisms, such as *Tribolium castaneum* (Herbst, 1797), *Drosophila melanogaster* Meigen (1830), and *Oncopeltus fasciatus* (Dallas, 1852). In beetles, *T. castaneum* has been the sole model in which to study evolutionary developmental mechanisms (Tomoyasu *et al.*, 2005). An exciting and relatively recent addition is *Onthophagus* (Scarabaeidae), which has emerged as a new model for examination of horn development utilizing several species within the genus (Moczek and Nagy, 2005; Moczek and Rose 2009; Moczek *et al.*, 2006, 2007). Although weevils are one of the most species-rich groups of organisms on the planet (ca. 60,000 species), and countless species are significant pests both of natural and agricultural landscapes, causing extensive damage (e.g. Ostmark, 1974; Saito *et al.*, 2005; Wilson *et al.*, 1996) and requiring extensive screening of imported agricultural products, not one weevil species has been utilized in developmental studies. The weevil rostrum is believed to represent a key innovation that has allowed the group to adapt and excel in phytophagy (e.g. Anderson, 1995; Toju, 2008), resulting in an extraordinary radiation (Anderson, 1995; Farrell, 1998; KcKenna *et al.*, 2009; Oberprieler *et al.*, 2007), diverse life histories, and a tremendous diversity in function and form. One of the most obvious and interesting topics to address in studying the evolution of this group is the formation of the rostrum and how it has differentiated throughout the major weevil lineages. From the fossil record, early weevil lineages, such as Eobelidae and the stem lineages of Nemonychidae from the Late Jurassic and Early Cretaceous, possessed elongate, nearly linear rostra, forms fairly different from extant ones. Throughout extant weevils, a wide range of rostral forms can be seen, ranging from several times longer than the body to more or less absent. Due to a scarcity in knowledge about the fundamentals of rostrum growth, which begins late in the last larval stage, traverses the pre-pupa, and continues throughout the pupal stage, this study has begun by investigating and documenting the morphological development of the rostrum in the rice weevil, *Sitophilus oryzae* (Linnaeus, 1763). Included is a description and review of the structure of the larval head capsule and adult rostrum to gain a comprehensive understanding of this process. The rice weevil has been chosen as a focal taxon primarily due to its agricultural significance (Cotton, 1920; Hardman, 1978; Hinds and Turner, 1911; Riudavets and Lucas, 2000) and relative ease in rearing compared to other pest weevil species. By thoroughly documenting and describing rostrum development and morphology in *S. oryzae*, it will serve as a comparison for examinations in other weevil lineages and as a foundation for conducting evolutionary developmental studies focusing on rostrum formation and genetic patterning, as has been the case in numerous other developmental systems (Moczek *et al.*, 2007; Prud'homme *et al.*, 2006; Martin and Reed, 2010; Reed and Serfas, 2004; Tomoyasu *et al.*, 2009).

Since the publication of various works on insect metamorphosis in the 19th century, such as Weismann's (1864) study of muscids, many other similar studies have appeared on various insect groups. Studies examining metamorphosis in weevils are few, particularly more so in those investigating rostrum development, and include works as Needham (1900), McClenahan (1904), Mansour (1927), Murray and Tiegs (1935), and to a lesser extent, Khan (1949). Of the studies that have focused on morphology and structure of the adult weevil head, including mouthparts (e.g. Bae, 1996; DuPorte, 1960; Lyal, 1995; Morimoto, 1962; Morimoto and Kojima, 2003; Morimoto, Kojima, and Miyakawa, 2006; Stickney, 1923; Ting, 1936; Williams, 1938), a few studies have excruciatingly detailed accounts of rostral structure and metamorphosis (e.g. Brack-Egg, 1973; Dennell, 1942; Dönges, 1954; Murray and Tiegs, 1935). Although it is not the aim of this study to provide such holistic descriptions of rostrum morphology in *S. oryzae*, it is important to highlight some of the more evident features, such as those seen in sagittal, frontal, and cross-sections, that are of possible phylogenetic utility when compared with other members in Curculionoidea and to summarize and build upon the outstanding work that has been already accomplished.

## 2. Materials and Methods

### *2.1 Rice weevil rearing*

A starter colony of *S. oryzae* was first obtained from Dr. Paul Flinn (USDA-ARS, Kansas State University). All stages were contained in plastic containers ~7 cm in width by 11 cm in height with breathing holes punctured through the lid, and reared on whole wheat kernels rather than rice (Fig. S1A; pers. comm. P. Flinn). Various larval stages and pupae were extracted from the wheat kernels (Fig. S1B) using a razor blade.

### *2.2 Histological sections + general microscopy*

All larvae, pupae, and adults used for histological examinations were first freshly killed in 95% alcohol, the head + prothorax (anterior half of the body in larvae) disarticulated from the body, and transferred to paraformaldehyde for ~1 day. The head + prothorax were then transferred to LR White (Electron Microscopy Sciences) for ~1 day. For embedding, body parts were placed in gelatin capsules filled to the top with LR White and then in an oven for ~24 hours at 60°C (thermal curing). After polymerizing, embedded specimens were removed from the capsules and sectioned using a Leica EM UC6 ultratome and diamond knife, producing thin sections ~5000–8000 nm thick. Sections were transferred to glass slides by heating them on a slide warmer for ~30 minutes followed by staining in either azure II, toluidine blue, hematoxylin + eosine Y, or DAPI. Sections stained in azure II, toluidine blue, or hematoxylin + eosine Y were digitally photographed with a Canon EOS-1 camera mounted on an Olympus BX51 compound microscope, and sections stained with DAPI were digitally imaged on a Zeiss Axioplan 2 upright epifluorescent microscope utilizing the software Slidebook (Intelligent Imaging Innovations), capturing the DAPI signal and autofluorescence of the weevil cuticle. The montage feature in Slidebook was utilized for whole-body imaging of the larvae. Regarding most photomicrographs, a z-stack was acquired of several images, combined using the software CombineZ, and edited in Adobe Photoshop CS3.

### *2.3 Electron microscopy*

Scanning Electron Microscope (SEM) images were captured using a LEO 1550 FESEM (Field Emission Scanning Electron Microscope). Specimens and dissections were mounted on SEM stubs using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite, and coating was performed using gold.

### *2.4 Terminology*

Many of the terms used for larval and pupal morphology follow May (1978). Terms applied for other life stages and certain head regions are cited in the relevant text. Many general terms, as they are applied, came from Snodgrass (1935).

## 3. Results

### *3.1 Biology of* Sitophilus oryzae *(Linnaeus), 1763 (rice weevil)*

Believed to have originated in India, *S. oryzae* was introduced into Europe early on where it was formally described by Linnaeus (1763). It is currently found to be cosmopolitan not only in the U.S. but also nearly worldwide. Reports of devastation in crop yield losses, in crops and stored grains such as rice, wheat, and corn (including many more), in the U.S. mostly reach back during the late 19th and early 20th centuries (Cotton, 1920). Today, as it has been the case for many decades, research continues on methods for reducing damage caused by this weevil (as well as associated congeners) (Batta, 2004; Riudavets and Lucas, 2000).

*Sitophilus oryzae* goes through four larval instars, a prepupal stage, and a pupal stage before reaching the adult (Figs. 1A, S1C). Individual holes near the surface of the plant tissue (such as corn or wheat) are excavated by the female's rostrum for each egg. After extending the ovipositor into the hole and depositing an egg, a plug is created by a fluid that is discharged from the ovipositor as it is withdrawn from the cavity and quickly hardens (Lathrop, 1914). Depending on the temperature, the eggs hatch approximately within three days (Hinds and Turner, 1911). The first three instars last approximately five days, while the fourth instar is slightly longer in duration, approximately 6-10 days (O'Donnell, 1967; Richards, 1947; Soderstrom, 1960). The prepupal stage is relatively short, though may last from 1-3 days. The pupal stage typically is approximately seven days, and the adult, on average, usually is 3-6 months (Cotton, 1920). These time intervals (Fig. 1A), of course, are highly variable depending on the time of year and mostly humidity and temperature. Rostrum development begins late in the fourth instar, with most tissue growth taking place during the prepupal and pupal stages.

### *3.2 Structure of the larval head capsule*

In order to better understand formation of the rostrum and why it takes the shape it does, as explained later, it is necessary to know the basic structure of the precursors in *S. oryzae*, namely the larval head capsule and some of its internal tissues. The larval head capsule is divided into three basic parts (frons and a divided epicranium) by ecdysial lines, laterally by the frontal lines and dorsally by the epicranial/coronal line. The cervix is the fairly membranous area connecting the head and thorax, with the anterior part more sclerotized and forming triangular flaps termed cervical plates. The head is strengthened by ventral sclerites, the tentorial bridge and hypopharyngeal bracon (Fig. S2A). Processes that protrude into the head include the enlarged, flattened, and blade-like abductor and adductor tendons of the mandible (particularly the adductor tendons) and an enlarged, sheet-like phragma from the posterior region of the epicranial line (here termed the epicranial phragma). These processes, though still present in early 4th instar (stadium) larvae, are digested during the interval from late 4th instar to prepupa. During apolysis in the transition from prepupa to pupa, the middle of the tentorial bridge and hypopharyngeal bracon also become weakened, where they break at ecdysis in conjunction with the splitting of the epicranium at the ecdysial lines. As the pupa emerges from the prepupal exuvia, it must also shed cuticle lining the interior of the fore- (stomodeum) and hindgut (proctodeum). Thus, because cuticle of the foregut remains in the prepupal head during development of the pupal head and proliferation of rostral tissue, a discernable empty tube is apparent in the developing rostrum and in thin sections taken during this stage (Figs. S2E, S4A).

### *3.3 Rostrum development*

#### 3.3.1 3rd instar larva (Figs. S2A–S2C)

This instar seems to be quite noticeable based on the relatively larger mandibles in relation to the head capsule (Fig. S2C). As larval tissue degredation and reformation does not begin until the 4th intar, at this time all internal structures are intact. The most notable structures in the head at this stage are the large cranio-mandibular muscles, namely the mandibular adductor and abductor muscles (Fig. S2C), as well as the cerebrum and suboesophageal ganglion (not figured).

### 3.3.2 4$^{th}$ instar larva

*3.3.2.1 Early* (Figs. 1B, 2A, S2D, S2E)*:* Through the beginning and middle of the fourth instar the larval digestive system and head structures (skeletal muscles, fat deposits) are still intact (Figs. S2D, S2E) and mouthparts remain functional. Prior to this instar, no adult tissues have formed and much of the larva is composed of fat bodies. During the early stages of the 4th instar, however, tissues that will form adult structures (legs, head appendages, wings, genitalia) begin to aggregate, differentiate from surrounding cells and become discernable from other cell masses and abundant larval fat bodies, and appear as compressing tissue folds.

*3.3.2.2 Middle* (Figs. 1C, 2B, S3)*:* While the imaginal tissues (wings, genitalia) begin to take shape and other adult structures (head and thoracic appendages) begin to develop as ectodermal outgrowths (they probably do not form as embryonic primordia and persist undifferentiated until metamorphosis [Sehnal *et al.*, 1996]; currently only some Diptera appear to derive all appendage growth from imaginal precursors [Angelini and Kaufman, 2005]), the onset of apolysis can be detected as the tissue of the prepupal head begins to retract slightly from the cuticular walls of the head capsule and form the subcuticular/ecdysial space (Heming, 2003; Figs. S3D–S3G). Towards the middle of the 4$^{th}$ instar, the developing pupal tissues also become slightly more discernable (Fig. S3). The antenna appears as a large tissue bud (Figs. S3A–S3C) and the epidermal tissue begins to proliferate and thicken, particularly at the mouthparts and antero-dorsal margins of the head (Figs. 1C, 2B, S3D–S3G). It is interesting that the early formation of the antenna in *S. oryzae* during this stage appears quite similar to that of the genitalia (particularly the aedeagus) in form. The tissue forming the adult legs appear to develop similar to those in other weevils (Needham, 1900), as well as the horns of scarab beetles (Moczek, 2005; Moczek and Nagy, 2005), as evaginated tissue folds (Figs. S4A, S4B, S4D, S4E).

*3.3.2.3 Late 4$^{th}$ instar/early prepupa* (Figs. 1D, 1E, 2C, S4)*:* It is somewhat difficult to discriminate between the 4$^{th}$ instar larva and an early prepupa, largely because there is no molt separating the two and the prepupal stage typically lasts only one to two days (Cotton, 1920). A definitive sign indicating that the prepupal stage has begun, however, is following the purging of all gut contents. Towards the end of the fourth instar, the larval tissue begins to become broken down, digested, and reabsorbed as the adult tissues proliferate. The tissues of the adult alimentary canal, midgut, and hindgut begin to differentiate from the larval tissues and proliferate, such as the proventriculus and mycetoma (accessory cell mass), which is partly derived from the larval epithelium of the mesenteron, eventually forming much of the mesenteric ceacae (Mansour, 1927; Murray and Tiegs, 1935). The mycetoma contains mycetocytes (or bacteriocytes) that house the *S. oryzae* primary endosymbiont (SOPE), a gram-negative bacterium that lives in the midgut (Gil *et al.*, 2008; Heddi *et al.*, 1998, 1999; Lefèvre *et al.*, 2004; Figs. S4A–S4C). It is also during the end of this instar that the rostral tissue begins to take shape. In the head, the rostrum begins to form antero-dorsally on the head as a thin, almost indistinguishable layer of proliferating epidermal cells (Figs. 1D, 2C, S4A, S4B, S4D, S4E). The epidermal cells along the entire anterior region of the head then begin to proliferate, forming a slight bulge anteriorly that includes the proliferating tissue of the mandible (Figs. 1E, S4D–S4F). Thus, it appears that rostrum formation begins first through patterning of the mouthparts, followed by rapid proliferation of the pre-oral tissue (mostly the epidermis) and subsequent compression and elongation of this tissue. In a sagittal section, immediately below the rostral and mandible tissue is the pharynx, and ventral to the pharynx is the developing maxilla and labium (Figs. S4D–S4F). The tissue of the antennae also begin to proliferate, forming bulges antero-dorsally and covering the eyes (Fig. S4C). Nearing the prepupal stage the leg tissues begin to rapidly grow and appear as distinct lobes (buds), clearly demarcating the thorax from the abdomen.

### 3.3.3 Prepupa

*3.3.3.1 Early* (Figs. 1F, 2D, S5–S6)*:* Aside from distinct thoracic limb buds, as mentioned above, the prepupal stage is also entered with an empty midgut, in which its contents have been extruded to prepare for the massive growth and reorganization of tissue during this stage. When the developing pupal epidermis largely retracts from the larval cuticle (particularly in the head and thorax), it is clear that the transition from 4$^{th}$ instar to prepupa has occurred (Figs. S5). It is also noticeable that this transition has occurred when the dorsal, large tissue bulge of the first larval thoracic segment (T1, fig. S4A) has diminished and no longer overlays the head capsule postero-dorsally (Fig. S5D). The remaining steps of pupal tissue degredation and rostral formation, and thus most tissue growth, occur during the prepupal stage. Through further cell proliferation, this thin layer becomes a distinct anterior tissue budding, the precursors of the adult mandibles, while the ventral portion of the rostrum (forming the adult maxillae and labium) also starts to proliferate (Figs. S5D, S5E). As this tissue mass grows (Figs. 1G, 2E, S6B-S6F), folds begin to appear in the developing pupal epidermis which becomes characteristically thickened. These pupal epidermal cells are elongate, with the nuclei situated dorsally and the thin cytoplasmic portion of the cell stretching to the basement membrane (Figs. S6, S8B, S8E, S8G).

*3.3.3.2 Late* (Figs. 1H, 2F, 2G, S7–S8)*:* Rapid cell proliferation continues in the head, in which the rostral epidermal tissue incorporates multiple folds between the mouthparts and its base (Figs. 1H, 2F, 2G, S7E–S7G, S8A-S8I) as a result of increased compression within the static volume of the larval head capsule. Due to the orientation of certain structures in the prepupal head capsule, features of the adult head and developing rostrum assume particular orientations that are very similar to those present in the prepupa. The larval tentorial bridge largely confines rostrum growth to within the head capsule (Fig S6C). The presence of the hypopharyngeal bracon (Fig. S6C) causes a rather deep cleft to form in the developing rostrum (Fig. S6B–S6D, S7G, S8C, S8D). The adult mandibles take shape on the dorsal side of this cleft (dorso-anteriorly of the hypopharyngeal bracon), in the same area as the larval mandibles, while the maxillae and labium form on the ventral side of the hypopharyngeal bracon, reaching through the space between the tentorial bridge and hypopharyngeal bracon and occupying the same area as the larval maxillae and labium. The majority of rostral tissue, then, is tightly compacted between its base and the larval mouthparts at the head apex. The antennae form closely oppressed to the head and covering the eyes (Figs. S7D–S7H). In sagittal section, the rostrum appears to be comprised of dorsal and ventral parts, an artifact due to the presence of the pharynx in the section plane (Figs. S5C–S5E, S6E, S6F, S8F, S8H–S8J, S8L). Before pupation the epidermal cells begin to secrete the pupal cuticle (Fig. S8E).

3.3.4 Pupa

*3.3.4.1 Early* (Figs. 1I, 2H, S9A–S9H)*:* At the onset of ecdysis, during emergence of the pupa from the prepupal exuvia (Figs. S9A–S9D), hydrostatic waves of haemolymph are forced anteriad in attempt to break the head capsule at the ecdysial lines. Once these lines are severed, higher pressure continues to be maintained in the head in order to free the pupal head from the larval head capsule. Though previously highly compacted, while the pupal head emerges from the larval head capsule, the rostrum immediately begins to elongate due to the hydrostatic pressure. Simultaneously shed with and attached to the head capsule, the foregut is slowly withdrawn from the unfolding pupal rostrum, which also assists in its extension by slightly pulling on the rostrum apically as it completely detaches from the prepupal epidermis. As the rostrum elongates and inflates with haemolymph, it is largely lacking any tissue due to the rapid expansion throughout the enlarged space of the once tightly compressed proliferating tissues in the prepupa.

*3.3.4.2 Middle-Late* (Figs. 1J, 2I, S9I–S9K, S10, S11)*:* Following ecdysis, the newly emerged pupa appears shriveled as the tissue in the appendages slowly expand (Fig. S9E–S9H). The epidermal tissue in the head, particularly in the antennae and rostrum, remains as thin, elongate cells (Figs. S10B, S10C) due to the rapid elongation and expansion of these parts after ecdysis and following rigid compression within the prepupal head capsule. As the pupal cuticle of the rostrum continues to expand and straighten the adult rostral and mouthpart tissues proceed to develop, eventually forming the pharynx, adductor and abductor tendons of the mouthparts (Figs. S10G, S10I), other smaller muscles distributed throughout the rostrum (pharyngeal dilators), and mouthparts (Figs. 2J, S10D, S10F, S10G, S10J, S10K, S11). Later in the pupal stage the tendons (essentially cuticular apodemes), in particular, beginning from invaginations of the ectodermal cuticle, become more visible as they proceed to lengthen towards the tentorium and head base (Figs. S10G, S10I, S11E–S11M). Their proximal ends are lined with columnar myoblasts which will attach to other groups of myoblasts at their future site of origin. At the base of the head, the developing tentorium and tendons (particularly the mandibular adductor and abductor tendons) appear quite similar, as they are both formed from cuticular invaginations (Figs. S11A–S11E). It is particularly interesting that even though the tentorium is formed by invaginating cuticle (Figs. S11A, S11B), the main part which usually remains connected to the ventral surface of the cranium, forming the gular suture(s), largely retracts internally in *S. oryzae*. The only parts of the tentorium that remain in contact to the cranial cuticle in the adult, then, are the posterior arms, which connect to the occipital foramen, the dorsal arms, which connect to the frons (adjacent to the compound eyes), and the slender ventral piece that forms the posterior tentorial pit (Fig. S16K). Towards the middle of the pupal stage most cuticular folds have become smooth and the pupal rostrum actually becomes slightly enlarged due to the influx of haemolymph (Figs. 2H, S9K, S10F, S10H). The rostral tissue that was highly compressed in the prepupa also continues to expand and lengthen. Towards the late pupal stage, the developing adult rostrum shrinks (Fig. 2I) as it approaches the final, slender form of the fully-grown adult, and the adult cuticle is secreted by the epidermal cells (Fig. S11D).

### *3.4 Structure of the adult head and rostrum (Figs. S12–S17)*

#### 3.4.1 General head morphology and regions (Figs. 3A-C, S17A–S17C):

Although the exact delimitations of various head regions are difficult to establish due to the fairly derived weevil head, as exemplified in *S. oryzae*, and the reduction and loss of sutures and sulci, approximations are certainly feasible in light of earlier works, particularly those of Dönges (1954), DuPorte (1960), and Lyal (1995).

Lineages that display more plesiomorphic features in the superfamily, in particular Nemonychidae, have features more similar to the other members of Phytophaga, and thus head regions that are more easily discerned. Such regions include the occiput (and postgena), pleurostoma (and gena), hypostoma, frons, and parietal. In *S. oryzae*, since the gula is more or less lost (except for its possible remnant embodied in the postgula), the parietals basically form most of the surface of the cranium. In weevils that possess a gula (defined by the gular/postoccipital sutures + subgenal sulci and the posterior tentorial pits), the occipital area is defined between these sutures and the occipital sulci, extending nearly to the apex of the rostrum. Because the occipital sulci have merged with the subgenal sulci in *S. oryzae* (Fig. 3D, S17D), the occiput is largely lost, except possibly for a narrow region around the occipital foramen. The presence of this occipital region is hypothesized largely based on the postgula containing a remnant of the gula. The postocciput, then, forms a narrow ring inside of the occiput and between the occiput and the postoccipital ridge. Because of the fusion of the gular sutures, a single posterior tentorial "pit" is visible as a shallow depression between the compound eyes. On the dorsal surface, although the frontal line is not distinct, considering the positions of the antennal insertions, the frons probably is somewhat triangular at its base, extends ventrally and surrounds the antennal scrobe, and possibly extends to the apex of the rostrum, dorsally. Also, because the epistomal (frontoclypeal) sulcus has been lost, as have been the anterior tentorial pits, the discernment of the clypeus is doubtful; however, as the rostrum structure appears to involve extension of elements basal to the mouthparts at least in *S. oryzae*, the clypeus would be presumed to occupy a reduced apical area of the rostrum. While the labrum is present in some basal curculionoid families, it too is absent in most weevils (including Dryophthoridae) and probably would also only occupy the extreme apex of the rostrum, if present at all.

Regarding the structure of the labium, the mentum and submentum basically are fused in Curculionoidea, leaving a distinct prementum and an uninterrupted sclerite posteriad. Although the anatomical differentiation of this posterior sclerite is ambiguous in weevils, the apical, projecting portion immediately posterior to the prementum is termed the postmentum. Through comparative morphology with other Coleoptera, particularly the sister group Chrysomeloidea, the submentum in weevils should begin immediately anterior of the posterior tentorial pit, extending apically until the postmentum (mentum). Considering where the submentum begins basally, the pleurostoma likely also begins at the base of the rostrum; however, it is also possible that the frons, or even a portion of the genal region of the parietals, may extend for a variable distance towards the rostral apex, leaving a small, apical pleurostomal region. In either case, the pleurostoma extends apically just before the mandibles (at the pleurostomal sinus), and possibly includes the outer margin of the hypostomal process (which is the distal extension of the postcoila), ventrally. The hypostoma forms most of the hypostomal process (or maybe all of it), the postcoila, and paracoila (Morimoto, Kojima, and Miyakawa, 2006), altogether forming a narrow region along the hypostomal sinus, adjacent to the postmentum.

### 3.4.2 Internal structures and morphology:

*3.4.2.1 Pharynx, oesophagous, tendons and muscles*: Generally, the pharynx extends from the distal end of the rostrum to the base of the rostrum approximately where the compound eyes are situated. Histologically, its extension is demarcated where the dorsal pharyngeal dilator muscles and pharyngeal plate end (just anterior to the circumoesophageal connectives), in which the pharyngeal circular muscles then also extend ventrally to fully encircle the oesophagous where it begins, characterized by its deep, longitudinal folds (Figs. S13F, S14A–S14C). As first mentioned by McClenehan (1904), the pharynx, similar to the hypopharyngeal bracons, is also densely lined with posteriorly-directed spines (Figs. S15D, S15E, S16C). Although some studies have mentioned the oesophagous as also possessing these spines (Ting, 1933) or neither the pharynx or oesophagous possessing spines (Dennell, 1942), they are clearly present on the dorsal and lateral cuticle of the pharynx and absent in the oesophagous (Fig. S16H) in *S. oryzae*. Thus, this feature may also demarcate the limits of the pharynx and oesophagous. The pharyngeal dilators are muscles that basically extend in two rows along the length of the pharynx and rostrum, dorsally (Figs. S11F–S11M, S13H–S13K). In sagittal and cross sections the large nuclei of the pharyngeal dilator muscle cells are readily visible (Figs. S11F–S11M, S12D, S12F). The pharyngeal circular muscles (ring muscles) extend the length of the pharynx and rostrum (Figs. S12E, S12J, S12K), dorsally and laterally, then continue on all sides completely enveloping the oesophagous, ending before the crop and proventriculus (Fig. S16I). The lateral pharyngeal connectives are muscles that function to fasten the pharynx in the lateral plane (Figs. S11J–S11L). The hypopharyngeal bracons are spiny processes just adjacent to and that envelope the mandibular adductor tendons basally (Figs. 2K, S11M, S14F–S14H, S14J–S14N, S15A-S15C, S16C, S16D). They then quickly diverge from the adductors and continue into the pharynx to nearly midway towards the base of the rostrum (Fig. S17I), where they assist in food uptake along with the rhythmic contraction of the dorsal pharyngeal dilators. In sagittal sections the large mandibular adductor (craniomandibularis internis; Figs. 2L, S12A, S12B, S12D, S12G–S12I) and abductor (craniomandibularis externus; Figs. 2L, S12A, S12B, S12D, S12E, S12G–S12K) muscles and associated tendons are quite distinct, the former attached dorsally and postero-dorsally in the cranium, and the latter arising from the ventral area of the head. In frontal and cross sections the adductor and abductor tendons reach nearly to the posterior margin of the head (Figs. S13), becoming elongate and flattened at the rostral base and into the cranium (Figs. S11A–S11C, S11E, S14A–S14C). Although the tendons reach into the cranium, the muscles only reach to approximately the base of the rostrum, thus also serving as a proxy for the delimitation of the head and rostral regions (Morimoto and Kojima, 2003). The adductor tendons, in addition to having a single, large tendon extending to the mandible, have a transverse plane situated at the anterior extension of the muscles (approximate junction of the cranium and rostrum), allowing for a greater surface area for attachment (Figs. S13C–S13F). The anterior extension of the dorsal tentorial arms can be seen connecting to cuticle adjacent to the eyes, mesally (Fig. S13C, S16J–S16L, S17F–S17H, S17K). Also in the frontal and cross sections, as in the sagittal sections, many of the maxillary muscles (Figs. S12E, S12I, S14A–S14C) and muscles attaching to the antennal scape (Fig. S11H, S13F) are visible. Slightly beyond the base of the rostrum and towards the apex, the maxillary tendons are small in comparison to the much larger mandibular tendons (Figs. S14D–S14J). In most extant Curculionoidea, in which the rostrum is fairly curved, most mouthpart tendons are situated in cuticular canals that guide and facilitate their sliding action. The canals for the larger mandibular tendons, naturally, are quite deep, and constitute apodemes or phragmata formed by the occipital sulci (Figs. S14D, S14E, S14G–S14J). In weevils that possess distinct subgenal sulci (such as *Rhynchites auratus*; Brack-Egg, 1973), separate phragmata are present for supporting the maxillary tendons. In *S. oryzae* the occipital sulci have merged with the subgenal sulci, and the phragmata of the subgenal sulci apparently have formed a bridge connecting the phragmata of the occipital sulci (which support the mandibular tendons; Figs. S14D, S14E, S14G–S14J). The tendons of the maxilla, then, rest in canals on this bridge (Figs. S15G–S15J). Nearing attachment to the mouthparts, as was the case at the base of the rostrum, the tendons take a more central position in the rostral cavity, eventually arriving adjacent to and partially enclosed by the pharyngeal bracons (Figs. S14I–S14M). Also at the apex, the pharynx widens, the pharyngeal bracons become more visible, and the posterior extensions of the mentum, which facilitate in guiding the mandibular tendons, are visible (Figs. S14J–S14N). Slightly further apically are the bases of the mandibles, the mandibular postartis (Fig. S12G), the body of the mentum and lateral extensions of the hypostoma, and eventually the maxillae (Figs. S14N–S14P).

*3.4.2.2 Tentorium*: The tentorium in *S. oryzae* consists of posterior arms, a dorsal bridge (to which the cibarial dilators attach, M48 [Figs. S15H, S16K]), and dorsal arms (Figs. S16J–S16L, S17F–S17H, S17K). The dorsal arms are a branching of the anterior arms, which are lost in the majority of Curculionoidea except for Belidae (Morimoto and Kojima 2003; Morimoto, Kojima, and Miyakawa, 2006). As mentioned above, the dorsal arms attach to an internal inflection of the cuticle that forms an ovoid phragma ventral to the compound eyes (Fig. 3E).

*3.4.2.3 Gula and postgula*: In primitive curculionoids the gula is present, in which the gular sutures (postoccipital sutures) form internal phragmata that constitute the tentorium. In *S. oryzae* the gula has been lost, including the gular sutures, and what appears to be the only trace of the gula is the small, triangular posterior sclerite termed the postgula. Although Lyal (1995) hypothesizes that the postgula is really equivalent to fused cervical sclerites, it is possible that this homology statement is incorrect. In the more basal curculionoid lineages, such as Nemonychidae, paired cervical sclerites in the neck membrane are indeed visible, but these sclerites are accompanied by what appears to be the postgular sclerite, which is the thin posterior margin of the gula. In lineages where the gular sutures fuse medially to form a single suture, this postgular sclerite is greatly reduced in size and often triangular; however, in such cases the paired cervical sclerites are often also present. In the remaining cases, such as in *S. oryzae*, the cervical sclerites appear to have fused with the postgula, thus forming a single triangular sclerite (Figs. 3E, S16J, S16K) where the cervical muscles originating from the prothorax attach. The remainder of the gular region anterior to the postgula, as in many higher weevils, is completely internalized (Figs. S16J–S16L) and the posterior tentorial "pits" are essentially fused into a single "pit" located ventrally, approximately midway between the compound eyes (Figs. S16K, S17D).

*3.4.2.4 Cuticle*: Through slightly oblique sagittal and frontal sections, the helicoidal array of chitin macrofibrils and structural layering of the cuticle are also readily visible (Figs. S12C, S15J, S16B, S16F, S16G). It is interesting to note that the cuticle along the rostrum appears slightly thicker than that of the head (Figs. S12H, S17F–S17K), most likely to give greater rigidity when circumscribing deep holes and while feeding on tough plant tissues.

## 4. Discussion

### *4.1 Evolutionary implications and significance*

While permitting detailed examination of rostrum tissue development from immature stages to the adult, this study gains insight into the development of phenotypic modifications that may incorporate genetic elements of head segmentation and appendage patterning. Although no invaginated imaginal tissue pockets (discernable as the discrete imaginal discs found in higher cyclorraphan flies [Angelini and Kaufman, 2005; Held, 2002; Kalm *et al.*, 1995; Younossi-Hartenstein *et al.*, 1993]) have been observed in *S. oryzae* or any other curculionoid, concentric tissue circles, similar to the imaginal discs of *Drosophila* before evagination, have been observed and are formed at least during the development of the legs. It has been mentioned that the wings and possibly genitalia may form somewhat loose imaginal discs (Tomoyasu *et al.*, 2005, 2009), and, indeed, several other types of tissue formations, ranging from external tissue growths to invaginated, stalked growths that resemble *Drosophila* imaginal discs, have been observed in coleopteran wings (Tower, 1903). The predominant type of appendage growth in Coleoptera, however, is the simple evaginated form, beginning with thickening of the epidermis and forming enlarged, compressed tissue buds within the larval cuticle (Needham, 1900; Powell, 1904). This evaginated type of epidermal growth is now well-known in giving rise to scarab beetle horns (Moczek, 2005; Moczek and Rose, 2009), which develop similarly to jointed appendages. It is also intriguing to note that Murray and Tiegs (1935) mention the rostrum of *S. oryzae* as developing from imaginal tissue. Although this observation cannot be confirmed here, it will be quite fascinating if developmental studies yield any indication of an overlap in modes of appendage patterning with rostrum formation.

Besides reviewing and further characterizing the structure of the weevil rostrum and its growth through successive developmental stages, this study was undertaken in order to initiate development of a weevil model for use in developmental biology, particularly in which the relationships between morphological change and structural genes responsible for phenotypic change can be examined in a phylogenetic context. In addressing this theme, weevil phylogeny has been thus far based largely on adult morphology (e.g. Kuschel, 1995; Marvaldi *et al.*, 2002; Morimoto, 1962), and to a lesser extent, on larval morphology (e.g. Marvaldi, 1997). Of those studies utilizing adult morphological characters, even fewer have focused on structures in the rostrum and head of the adult (Morimoto, 1962; Morimoto and Kojima, 2003). Comparisons of rostrum development among different taxa in a cladistic framework will serve to help elucidate weevil phylogeny, particularly in those groups that possess a rostrum but are currently not included within Curculionidae *s. str.* (e.g. Brentidae, Attelabidae, Nemonychidae, etc.; Alonso-Zarazaga and Lyal, 1999), as well as those groups that do not possess a rostrum and are sometimes contentiously included within Curculionidae *s. str.* (e.g. Platypodinae, Scolytinae). According to preliminary studies on the external and internal structure of the adult rostrum across Curculionoidea (Davis in prep.), it is apparent that even though the rostrum is superficially similar in external appearance, it has undergone substantial change throughout the various weevil lineages. Furthermore, although the ventral sulci of the rostrum also undergo great change, often fusing and causing a reduction in their number, the internal morphology of the rostrum (such as the costae and phragmata/apodemes that support the tendons of the mouthparts, in which their presence are most often demarcated by external sulci) does not necessarily demonstrate similar change. Thus, examination of rostrum structure and development, as with any morphological features, also will have remarkable influence on understanding homology statements, particularly when the relevant genetic elements involved in forming those structures are analyzed in comparison (Prud'homme *et al.*, 2006).

Future directions will focus on examining rostrum development in a diverse array of representatives across Curculionoidea, including sister-groups for comparison. Much like contemporary works studying development of beetle horns (Emlen *et al.*, 2007; Moczek and Rose, 2009; Moczek *et al.*, 2007), successive stages stemming from this morphological research will focus on a similar trajectory in determining specific genes that function directly in rostrum growth and differentiation, working towards elucidating the genetic pathways leading to formation of a rostrum. While formation of a rostrum may coincide with certain aspects of mouthpart development, because it is mostly composed of several elongated head sclerites, its developmental trajectory could more closely follow that of other forms of head extensions, such as eye stalk formation in diopsid flies (Hurley *et al.*, 2001; Warren and Smith, 2007), an appendage (Angelini and Kaufman, 2005), or cuticular horn as mentioned before. It would be possible to suggest specific genes or pathways that potentially are responsible for rostrum formation, such as those recognized in the studies of the structures mentioned above; however, given the great diversity of mechanisms by which such structures may arise, it is probably most appropriate to await preliminary genetic data.

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## Figure legends

**Fig. 1**. Photomicrographs. A, developmental life stages and approximate stage durations of *S. oryzae*, showing 4 larval instars, a prepupal stage, pupa, and adult; B-J, diagrams of sagittal sections illustrating rostrum growth from early 4$^{th}$ instar larva to late pupa; colors: black = cuticle, green = muscle tissue, blue = epidermis, red = nervous tissue. B, early 4$^{th}$ instar larva; C,

middle 4th instar larva; D-E, late 4th instar larvae; F, early prepupa; G, middle prepupa; H, late prepupa; I, early pupa; J, late pupa.

**Fig. 2**. A, photomicrograph of early 4th instar larval head and thorax, sagittal section visualized with DAPI and autofluorescence; B, middle 4th instar larval head and thorax, sagittal section stained with toluidine blue (same staining also in B, C, D, E, F, H, I, J, K, L); C, late 4th instar larval head and thorax, sagittal section stained with toluidine blue; D, early prepupal head, sagittal section stained with toluidine blue; E, middle prepupal head, sagittal section stained with toluidine blue; F, late prepupal head, sagittal section stained with toluidine blue; G, SEM micrograph of late prepupal head, anterior view; H, early pupal head and thorax, sagittal section stained with toluidine blue; I, late pupal head and thorax, sagittal section stained with toluidine blue; J, late pupal rostrum, cross section stained with toluidine blue; K, adult rostrum, cross section stained with toluidine blue; L, adult head, sagittal section stained with toluidine blue.

**Fig. 3**. A-C, SEM micrographs of adult heads with color coded regions according to legend in box. A, dorsal view; B, anterior view; C, ventral view. D, SEM micrograph, enlargement of ventral view of rostrum; E, illustration of dorso-lateral view of cranium, with lateral window excised to expose tentorium.

**Supplement Figure legends**

**Fig. 1**. Photomicrographs. A, Adult *S. oryzae* feeding on whole wheat kernels; B, a prepupa removed from its pupation chamber in a wheat kernel; C, developmental life stages of *S. oryzae*, showing 4 larval instars, a prepupal stage, pupa, and adult.

**Fig. 2**. A-B, SEM micrographs. C-E, epifluorescent micrographs. A, head capsule of 3rd instar larva, ventral view; B, enlargement of anterior region in 4; C, sagittal section of anterior half of

3rd instar larva, visualized with DAPI (green) and autofluorescence (red); D, sagittal section of head of early 4th instar larva, visualized with DAPI (green) and autofluorescence (yellow); E, sagittal section of early 4th instar larva, grayscale image visualized with DAPI and autofluorescence.

**Fig. 3**. A–G, sagittal sections of heads of middle 4th instar larvae, arrows indicating differentiating and thickening epidermal tissue. A–D, photomicrographs, sections stained with toluidine blue. E–G, epifluorescent micrographs. H, section legend (SEM micrograph).

**Fig. 4**. A–F, sagittal sections of late 4th instar larvae, arrows indicating differentiating and thickening epidermal tissue. A–D, photomicrographs, sections stained with toluidine blue. A, whole larva; B–D, anterior of larvae. E–F, epifluorescent micrographs. E, anterior of larva; F, anterior of head. G, section legend (SEM micrograph).

**Fig. 5**. A–E, photomicrographs of sagittal sections of early prepupae, sections stained with toluidine blue. A–C, E, heads of prepupa; D, anterior half of prepupa. F, section legend (SEM micrograph).

**Fig. 6**. A–F, photomicrographs of sagittal sections of heads of middle prepupae, sections stained with toluidine blue. G, section legend (SEM micrograph).

**Fig. 7**. SEM micrographs of late prepupa. A–C, late prepupae with larval cuticle and head capsule intact. A, lateral view of entire prepupa; B, ventral view of head and prothorax; C, anterior view of head capsule. D–H, late prepupae with larval cuticle and head capsule removed. D, lateral view of head and thorax; E, enlargement of head and prothorax of D; F, anterior view of head; G, ventral view of head and prothorax; H, dorsal view of head and prothorax.

**Fig. 8**. A–L, photomicrographs of sagittal sections of late prepupae, sections stained with toluidine blue. A, head; B, enlargement of dorsal rostral tissue in A; C–D, heads; E, enlargement

of dorsal rostral tissue in D; F, head; G, enlargement of ventral rostral tissue in F; H–I, heads; J, enlargement of pharynx in I; K, dorsal rostral tissue; L, head and thorax of prepupa; M, section legend for A–L (SEM micrograph). N, photomicrograph of frontal section of late prepupa, section stained with toluidine blue. O, section legend for N (SEM micrograph).

**Fig. 9**. SEM micrographs. A–D, prepupal-pupal transition. A, ventral view; B, enlargement of head and prothorax in A; C, lateral view; D, enlargement of head in C. E–H, early pupa. E, ventral view; F, enlargement of head and thorax in E; G, lateral view; H, enlargement of head in G. I–K, middle pupa. I, ventral view; J, enlargement of head and thorax in I; K, lateral view.

**Fig. 10**. A–L, photomicrographs of sagittal sections of pupae, sections stained with toluidine blue. A–D, middle pupae. A, head and base of rostrum; B, head, rostrum, and thorax, arrow indicating thickened epidermal cells; C, head, rostrum, and thorax; D, apex of rostrum. E–L, late pupae. E–F, head, rostrum, and prothorax; G, enlargement of apex of rostrum in F; H, head, rostrum, and prothorax; I, head and base of rostrum; J–K, apex of rostrum; L, head and rostrum. M, section legend for A–L (SEM micrograph).

**Fig. 11**. A–M, photomicrographs of cross sections of the pupal rostrum, sections stained with toluidine blue. N, section legend (SEM micrograph).

**Fig. 12**. A–K, photomicrographs of sagittal sections of adult heads, sections stained with toluidine blue. A-B, head and base of rostrum; C, enlargement of rostrum, arrows indicating helicoidal structure of cuticular chitin; D, head and rostrum; E, enlargement of base of rostrum in I; F, enlargement of middle part of rostrum in D, arrows indicating the large nuclei of the pharyngeal dilator muscle cells; G, enlargement of apex of rostrum in D; H, head and rostrum, arrows indicating different thicknesses of cuticle in cranium and rostrum; I, head and base of rostrum; J, rostrum; K, base of rostrum. L, section legend (SEM micrograph).

**Fig. 13**. A–K, photomicrographs of frontal sections of adult heads, sections stained with toluidine blue, except for C, stained with eosin Y. L, section legend (SEM micrograph).

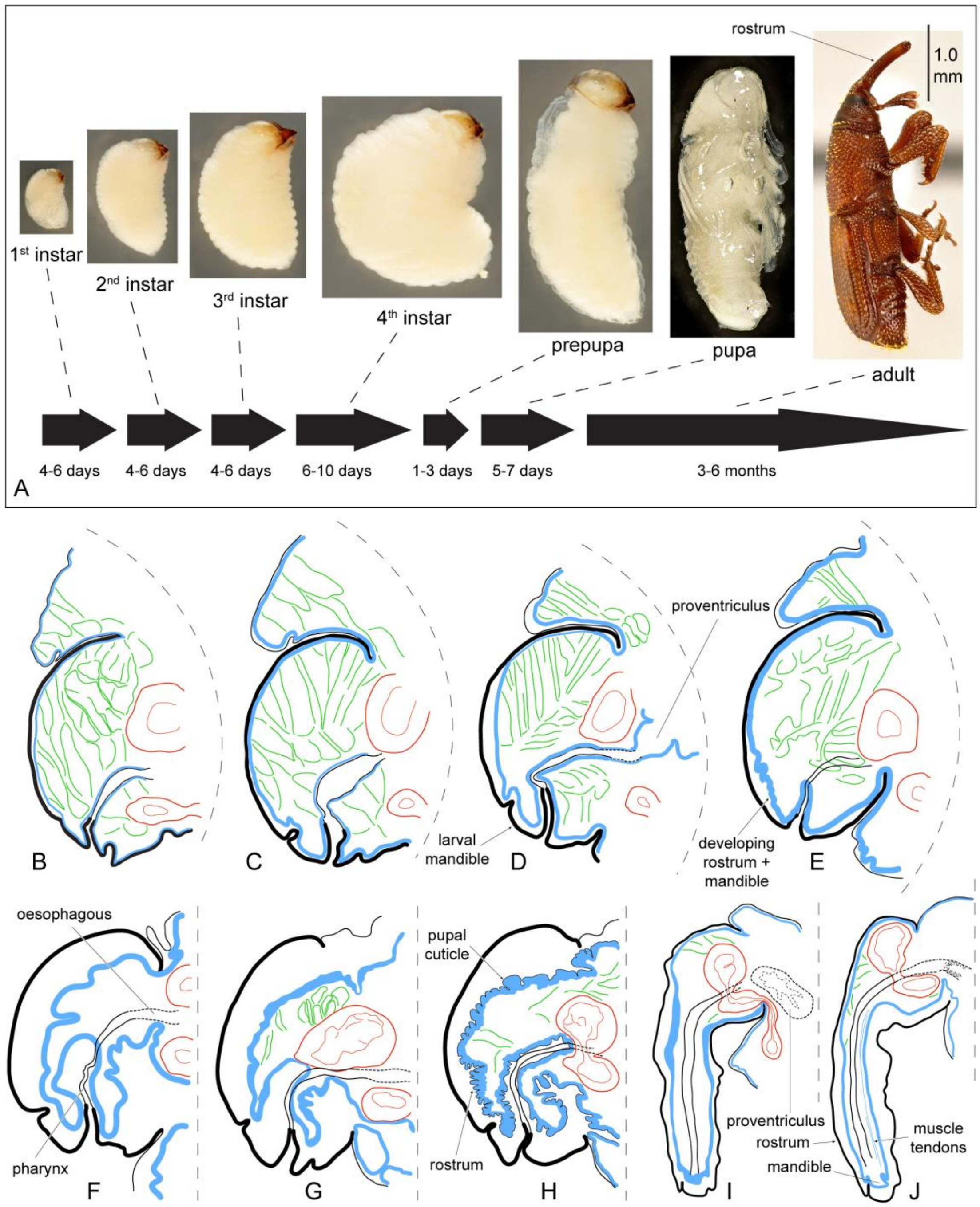
**Fig. 14**. A–P, photomicrographs of cross sections of the adult rostrum, sections stained with toluidine blue. Q, section legend (SEM micrograph).

**Fig. 15**. SEM micrographs of adult rostra in cross section. A–E, rostra were preserved in ~90% EtOH and air dried before cutting with razor blade. A, rostrum cut in cross section, image taken with In-Lens detector; B, same image in A but taken with SE2 detector; C, enlargement of rostral center in B; D, rostrum cut in cross section; E, enlargement of pharyngeal area in D. F–J, rostra were heated in KOH for ~30 minutes and air dried before cutting with razor blade. F–G, rostra cut in cross section; H, enlargement of central area and inner floor of rostrum in G; I, rostrum cut in cross section; J, enlargement of central area and inner floor of rostrum in I.

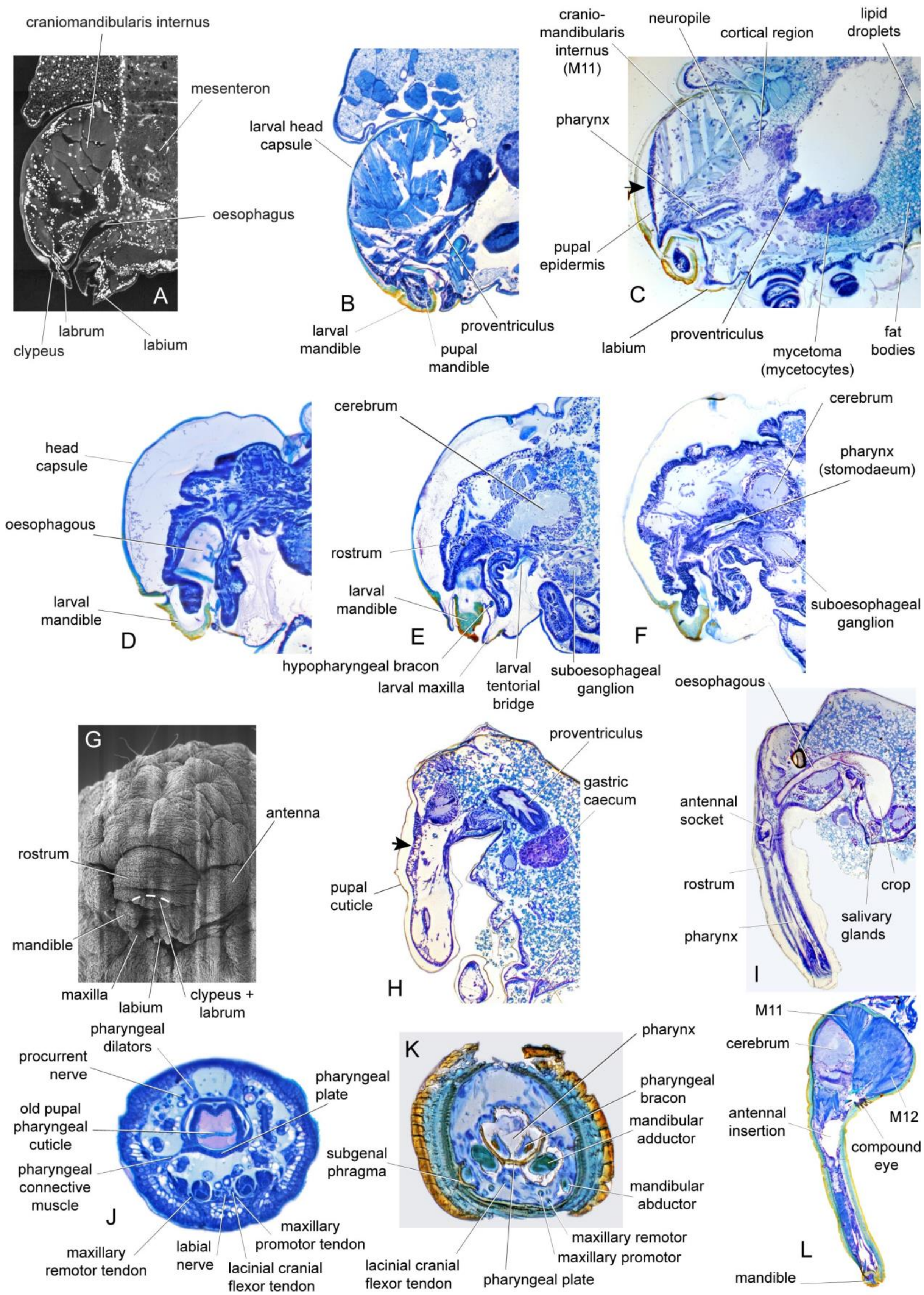
**Fig. 16**. A–J, L, SEM micrographs of adult head structures. A–G, rostra cut in cross sections; rostra were preserved in ~90% EtOH and air dried before cutting with razor blade. A, rostrum in cross section; B, enlargement of rostral cuticle in A; C, enlargement of pharyngeal area in A; D, enlargement of pharyngeal plate and pharyngeal bracons in C; E, rostrum in cross section; F–G, enlargements of rostral cuticle in E. H, cranium divided in cross section. I, proventriculus and crop (air dried from ~90% EtOH). J, dorso-lateral view of cranium, with lateral window excised using a razor blade to expose tentorium. K, illustration of lateral view of J. L, lateral view of J.

**Fig. 17**. SEM micrographs of adult head structures. A–C, adult heads with color coded regions according to legend in box. A, dorsal view; B, anterior view; C, ventral view. D, enlargement of ventral view of rostrum; E, posterior view of cranium exposing occipital (magnum) foramen; F, dorsal view of head, with dorsal window excised using a razor blade to expose interior of cranium and rostrum; G, enlargement of cranium-rostral base junction in F; H, enlargement of

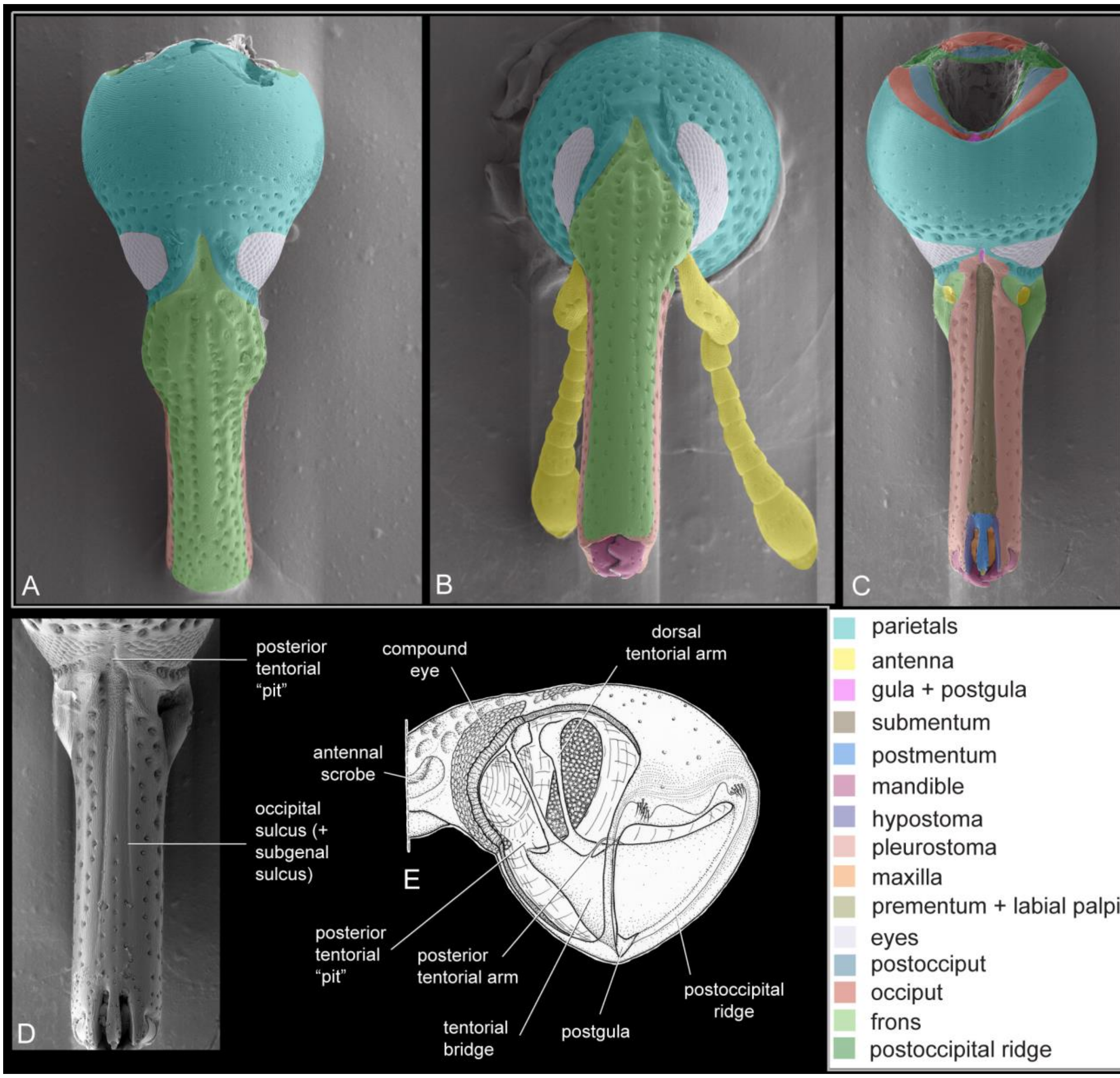
cranium in F; I, enlargement of rostrum in F; J, enlargement of rostral cutical in F; K, enlargement of dorsal tentorium arm-cranium junction in F.



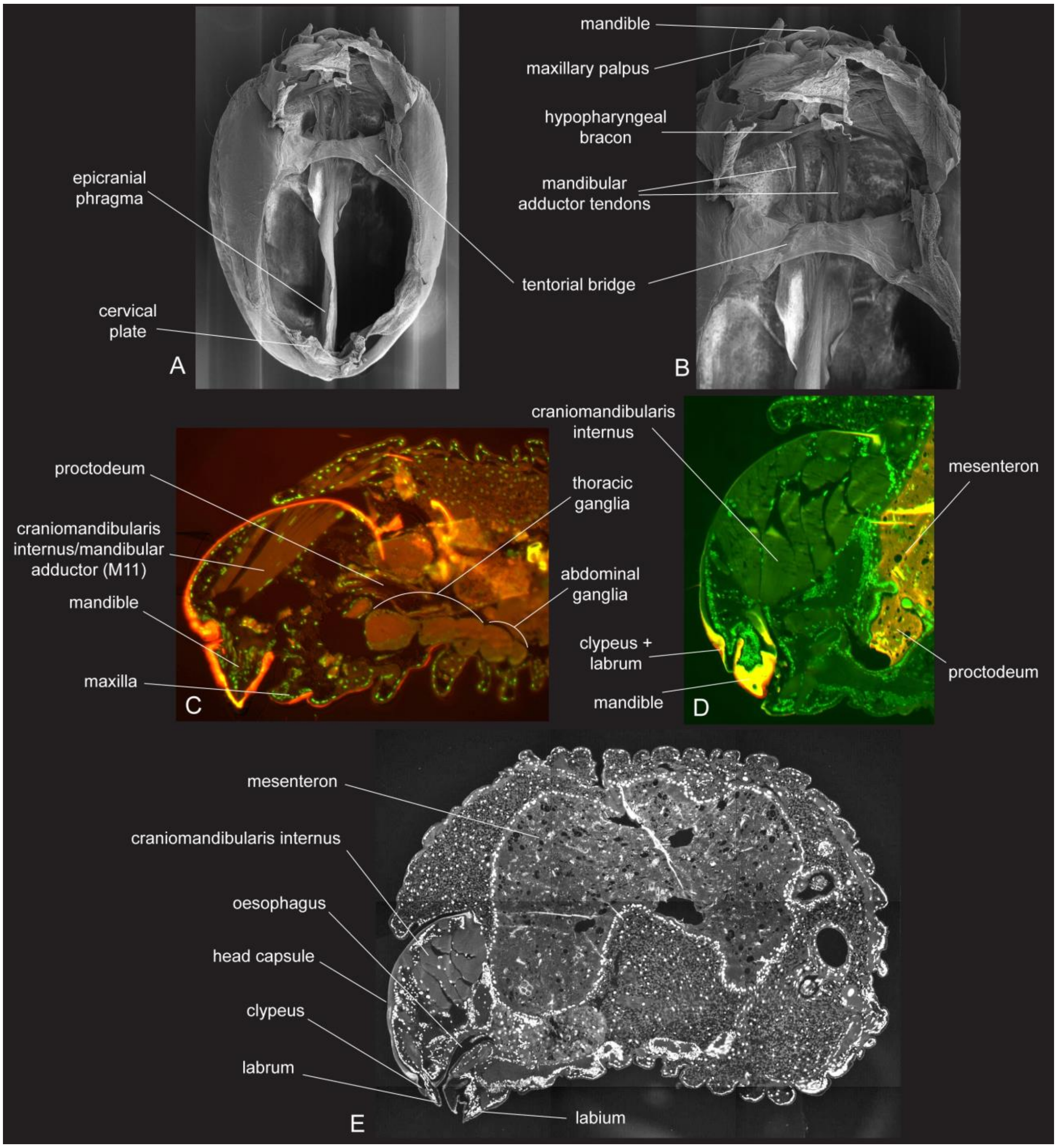
rostrum
1.0 mm
1st instar
2nd instar
3rd instar
4th instar
prepupa
pupa
adult
4-6 days
4-6 days
4-6 days
6-10 days
1-3 days
5-7 days
3-6 months
A
proventriculus
larval mandible
developing rostrum + mandible
B
C
D
E
oesophagous
pharynx
F
G
pupal cuticle
rostrum
H
proventriculus
rostrum
muscle tendons
mandible
I
J

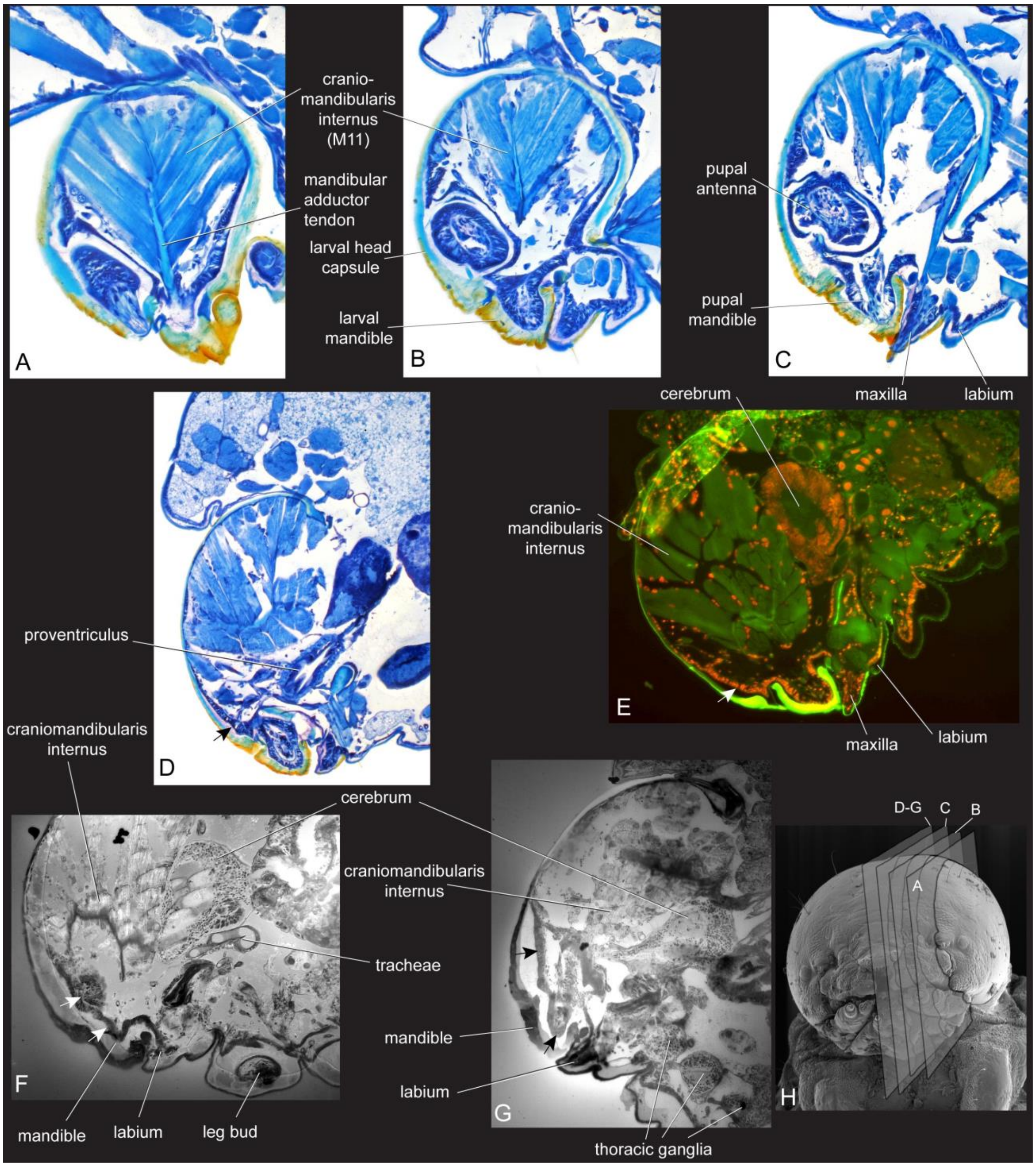


craniomandibularis internus
mesenteron
oesophagus
A
clypeus
labrum
labium
larval head capsule
B
larval mandible
pupal mandible
proventriculus
cranio-mandibularis internus (M11)
neuropile
cortical region
lipid droplets
pharynx
pupal epidermis
C
labium
proventriculus
mycetoma (mycetocytes)
fat bodies
head capsule
oesophagous
larval mandible
D
cerebrum
rostrum
larval mandible
E
hypopharyngeal bracon
larval maxilla
larval tentorial bridge
suboesophageal ganglion
cerebrum
pharynx (stomodaeum)
F
suboesophageal ganglion
G
antenna
rostrum
mandible
maxilla
labium
clypeus + labrum
proventriculus
gastric caecum
pupal cuticle
H
oesophagous
antennal socket
rostrum
pharynx
crop
salivary glands
I
pharyngeal dilators
procurrent nerve
pharyngeal plate
old pupal pharyngeal cuticle
pharyngeal connective muscle
J
maxillary remotor tendon
labial nerve
lacinial cranial flexor tendon
maxillary promotor tendon
K
pharynx
pharyngeal bracon
mandibular adductor
subgenal phragma
mandibular abductor
maxillary remotor
maxillary promotor
lacinial cranial flexor tendon
pharyngeal plate
M11
cerebrum
antennal insertion
M12
compound eye
L
mandible

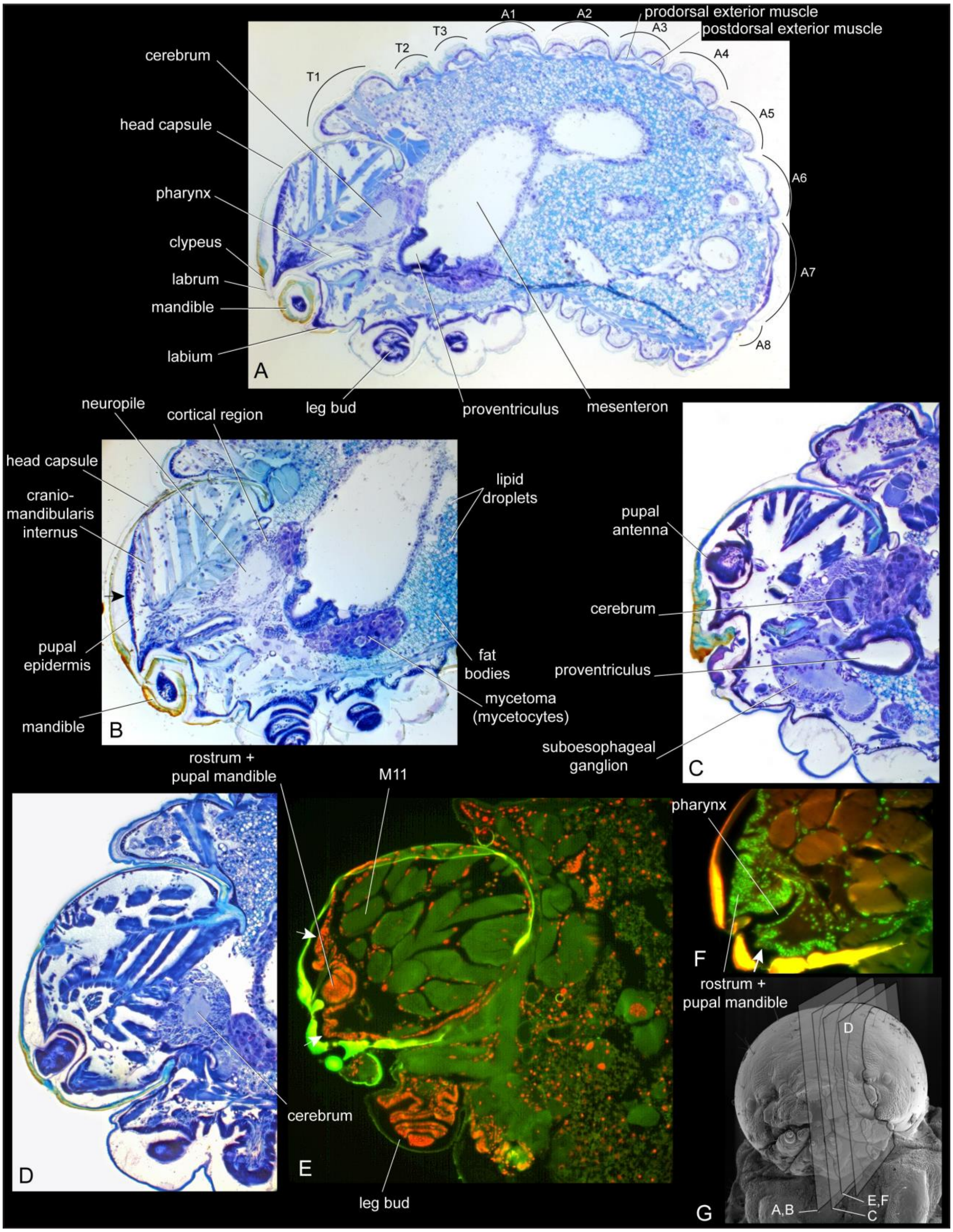

A
B
C
D
E
posterior
tentorial
"pit"
occipital
sulcus (+
subgenal
sulcus)
compound
eye
dorsal
tentorial arm
antennal
scrobe
posterior
tentorial
"pit"
posterior
tentorial arm
tentorial
bridge
postgula
postoccipital
ridge
parietals
antenna
gula + postgula
submentum
postmentum
mandible
hypostoma
pleurostoma
maxilla
prementum + labial palpi
eyes
postocciput
occiput
frons
postoccipital ridge

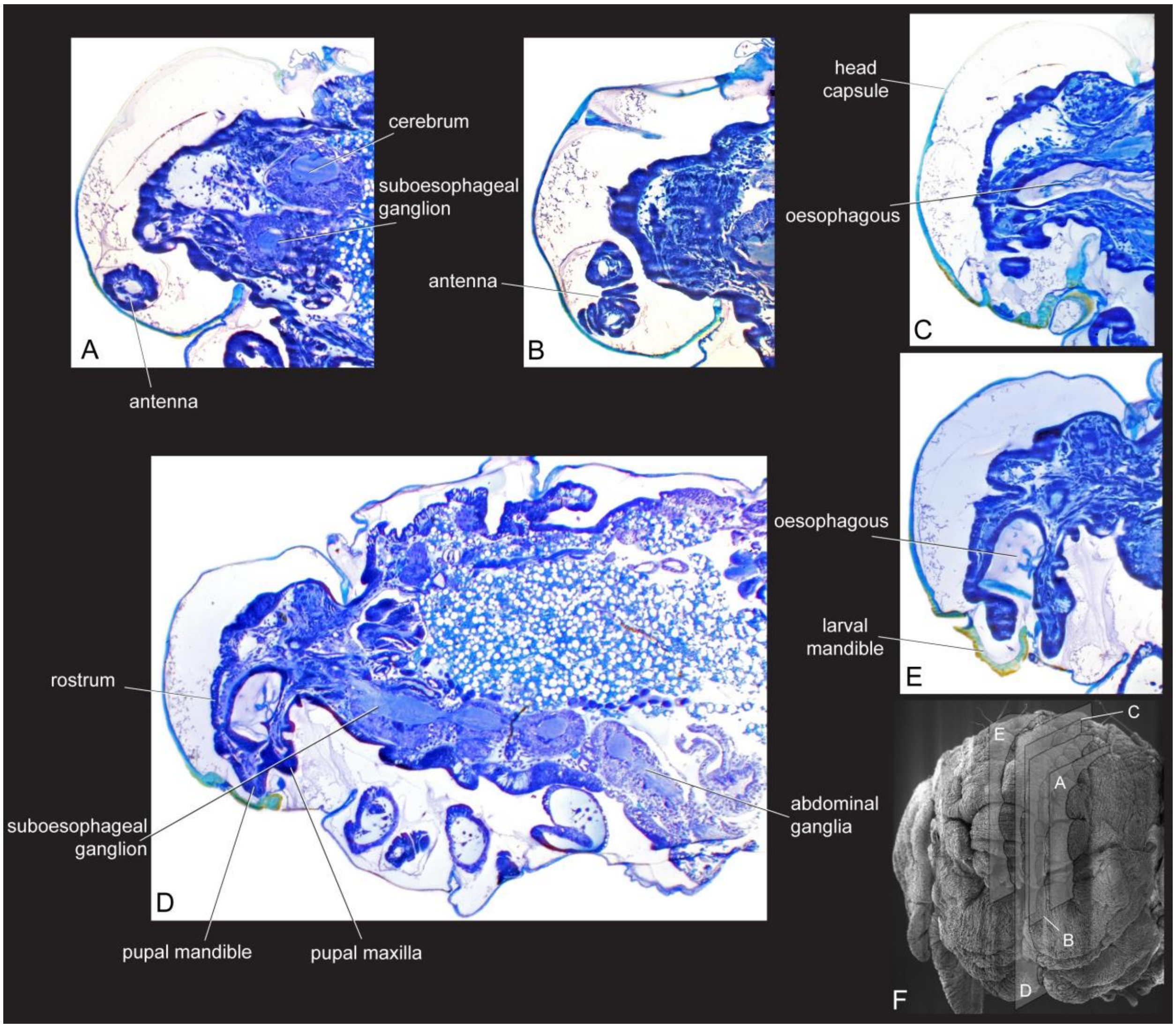

A
B
C
1st instar
2nd instar
3rd instar
4th instar
prepupa
pupa
adult

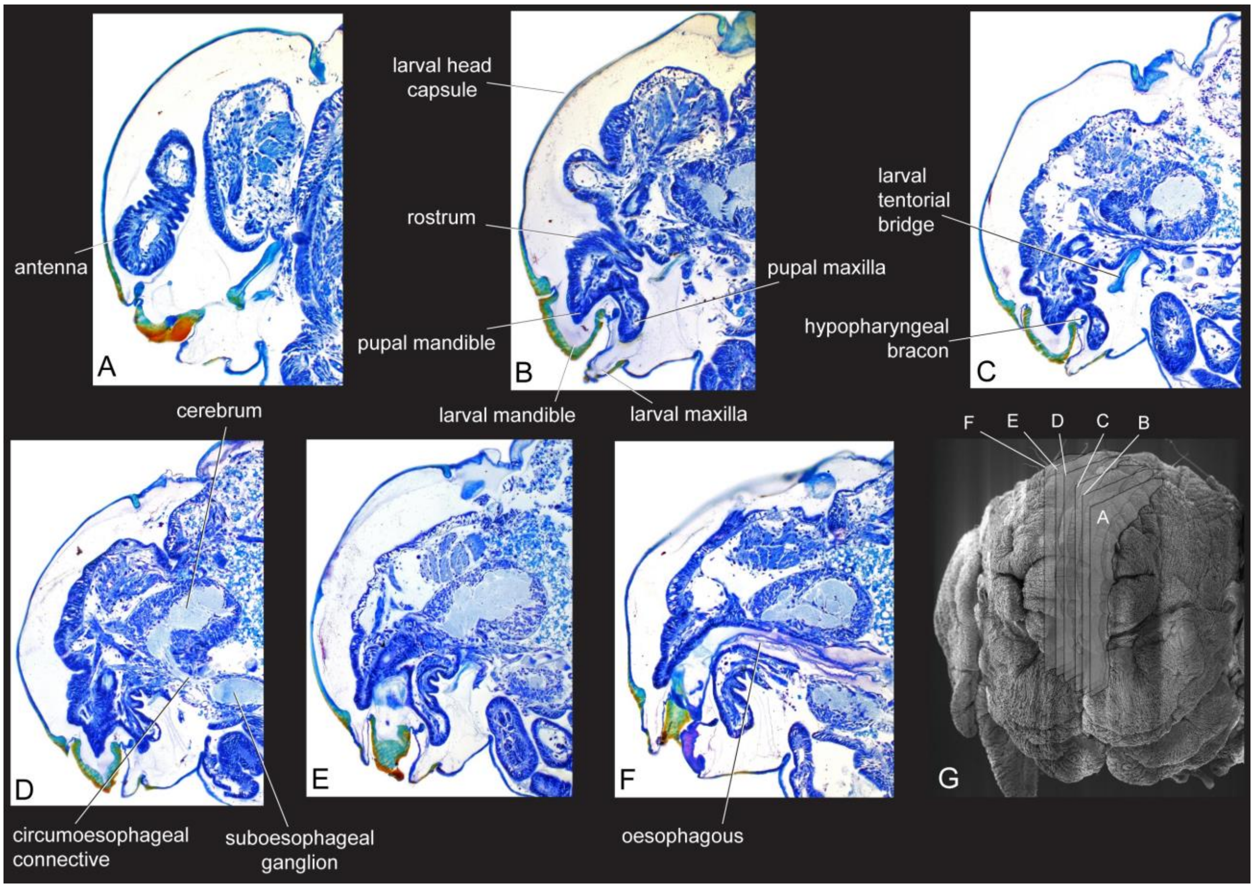

epicranial
phragma
cervical
plate
A
mandible
maxillary palpus
hypopharyngeal
bracon
mandibular
adductor tendons
tentorial bridge
B
proctodeum
craniomandibularis
internus/mandibular
adductor (M11)
mandible
maxilla
C
thoracic
ganglia
abdominal
ganglia
craniomandibularis
internus
mesenteron
clypeus +
labrum
mandible
proctodeum
D
mesenteron
craniomandibularis internus
oesophagus
head capsule
clypeus
labrum
labium
E

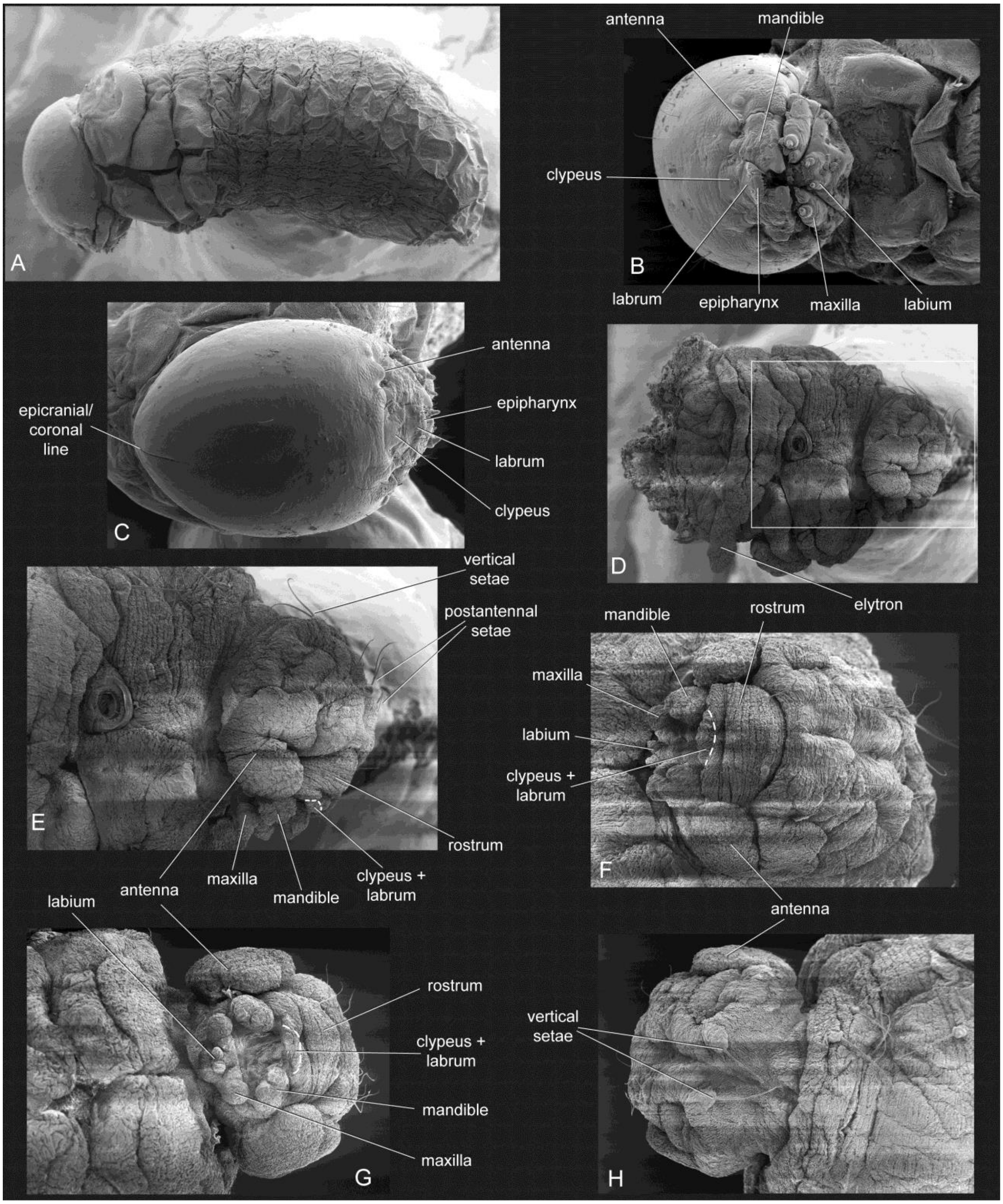


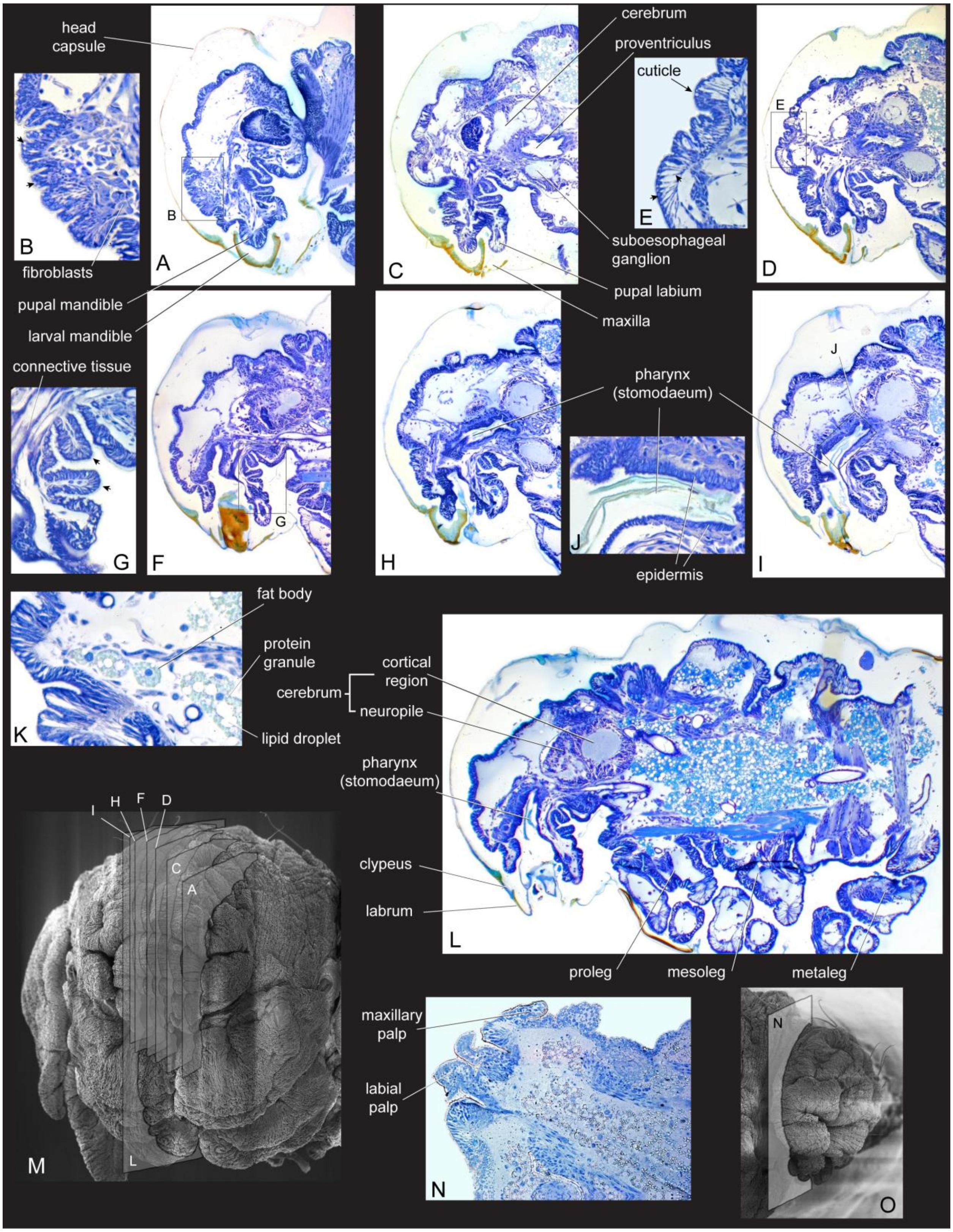
cranio-
mandibularis
internus
(M11)
mandibular
adductor
tendon
larval head
capsule
larval
mandible
pupal
antenna
pupal
mandible
maxilla
labium
A
B
C
cerebrum
cranio-
mandibularis
internus
proventriculus
maxilla
labium
D
E
craniomandibularis
internus
cerebrum
craniomandibularis
internus
tracheae
mandible
labium
mandible
labium
leg bud
thoracic ganglia
D-G
C
B
A
F
G
H

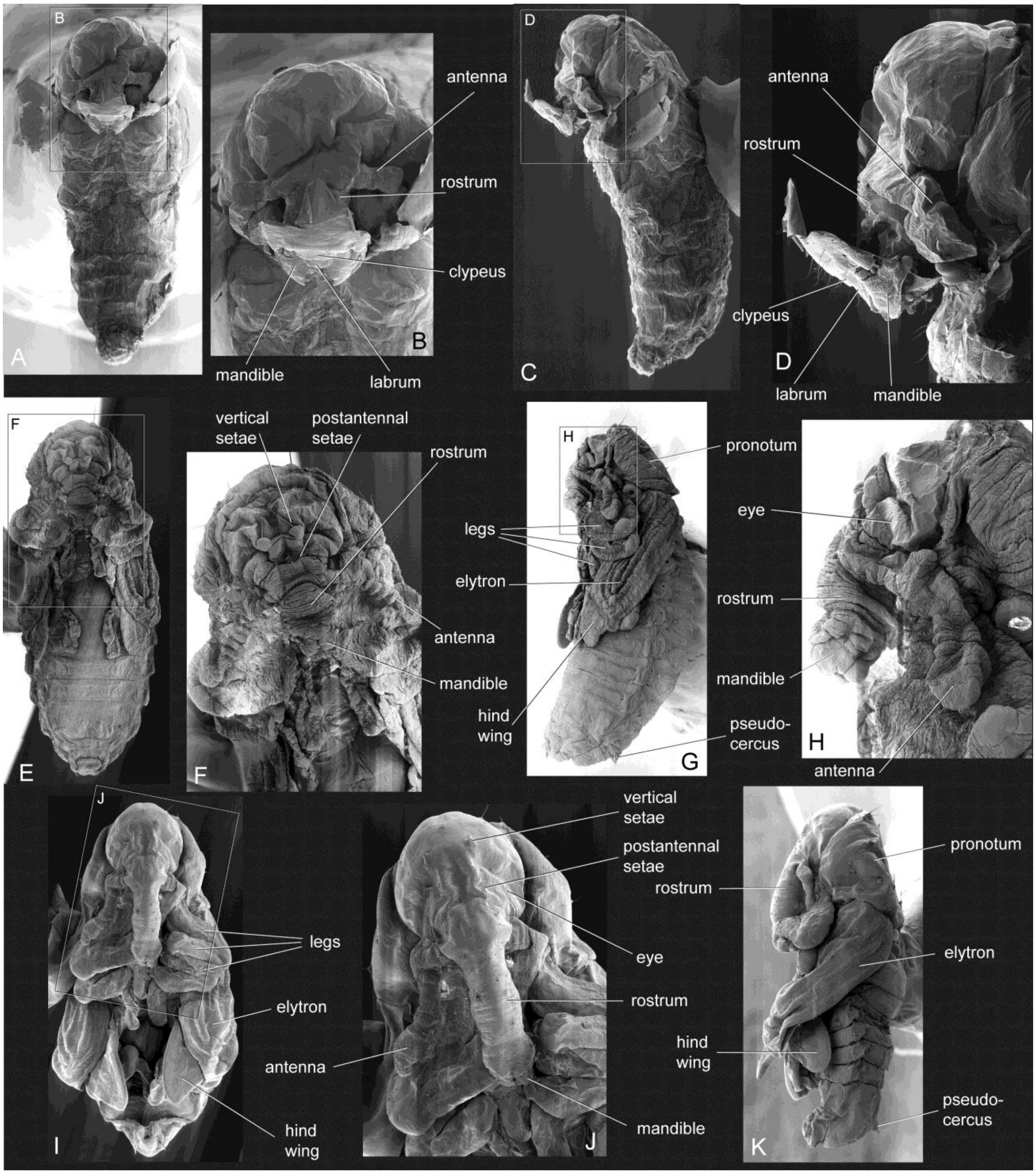

A
T1
T2
T3
A1
A2
A3
A4
A5
A6
A7
A8
prodorsal exterior muscle
postdorsal exterior muscle
cerebrum
head capsule
pharynx
clypeus
labrum
mandible
labium
leg bud
proventriculus
mesenteron
B
neuropile
cortical region
head capsule
cranio-
mandibularis
internus
pupal
epidermis
mandible
lipid
droplets
fat
bodies
mycetoma
(mycetocytes)
C
pupal
antenna
cerebrum
proventriculus
suboesophageal
ganglion
D
cerebrum
E
rostrum +
pupal mandible
M11
leg bud
F
pharynx
rostrum +
pupal mandible
G
D
A,B
E,F
C


cerebrum
suboesophageal ganglion
A
antenna
antenna
B
head capsule
oesophagous
C
oesophagous
larval mandible
E
rostrum
suboesophageal ganglion
D
pupal mandible
pupal maxilla
abdominal ganglia
E
C
A
B
D
F

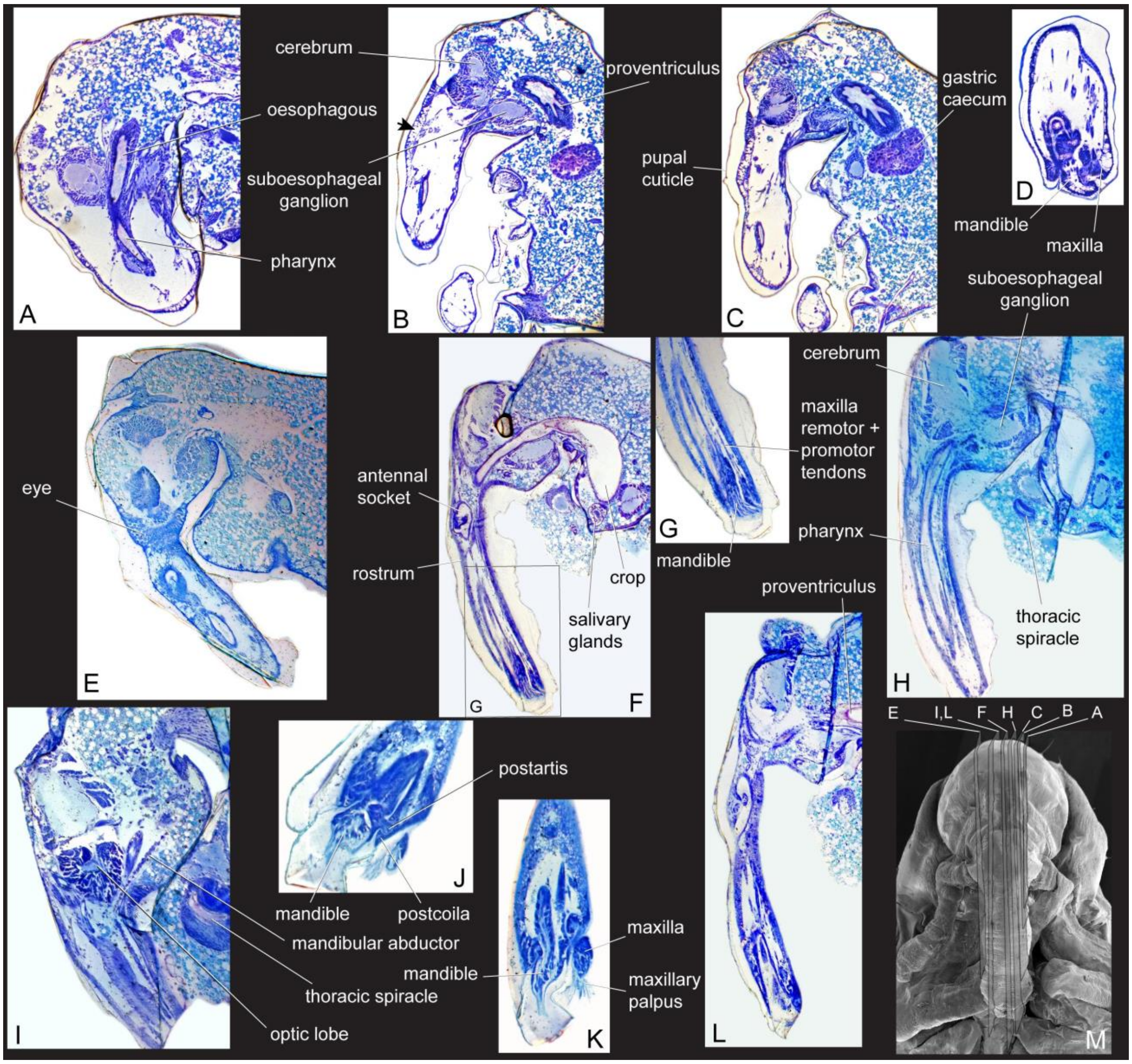

larval head
capsule
rostrum
pupal maxilla
pupal mandible
larval mandible
larval maxilla
antenna
larval
tentorial
bridge
hypopharyngeal
bracon
cerebrum
circumoesophageal
connective
suboesophageal
ganglion
oesophagous
A
B
C
D
E
F
G


A
antenna
mandible
clypeus
B
labrum
epipharynx
maxilla
labium
antenna
epicranial/
coronal
line
epipharynx
labrum
clypeus
C
D
elytron
vertical
setae
postantennal
setae
E
rostrum
antenna
maxilla
mandible
clypeus +
labrum
mandible
rostrum
maxilla
labium
clypeus +
labrum
F
antenna
labium
antenna
rostrum
clypeus +
labrum
mandible
maxilla
G
vertical
setae
H

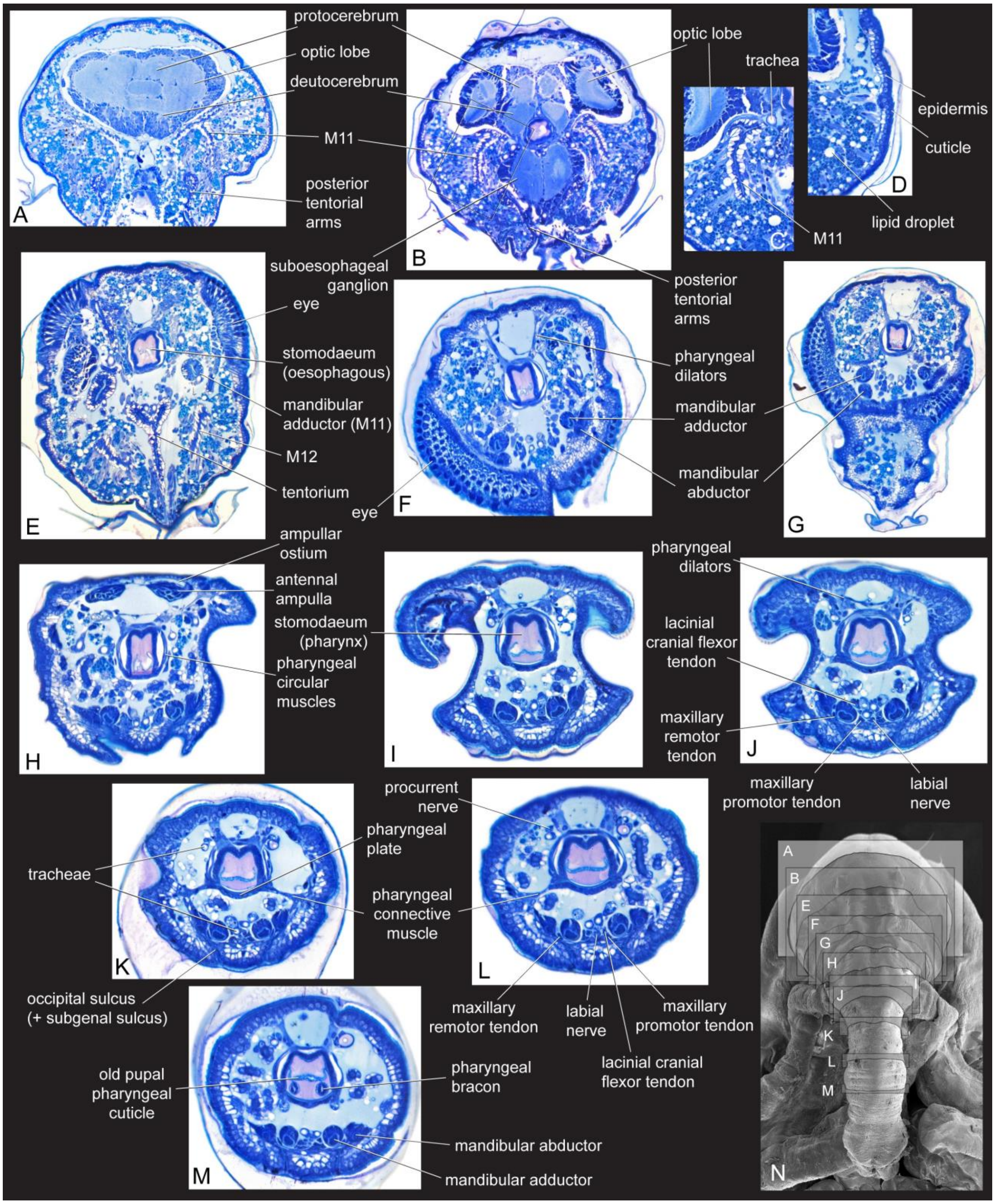

head capsule
B
fibroblasts
A
B
cerebrum
proventriculus
cuticle
E
E
C
suboesophageal ganglion
D
pupal mandible
larval mandible
pupal labium
maxilla
connective tissue
G
F
G
H
pharynx (stomodaeum)
J
J
epidermis
I
fat body
protein granule
lipid droplet
K
cortical region
cerebrum
neuropile
pharynx (stomodaeum)
clypeus
labrum
L
proleg
mesoleg
metaleg
I
H
F
D
C
A
M
L
maxillary palp
labial palp
N
N
O



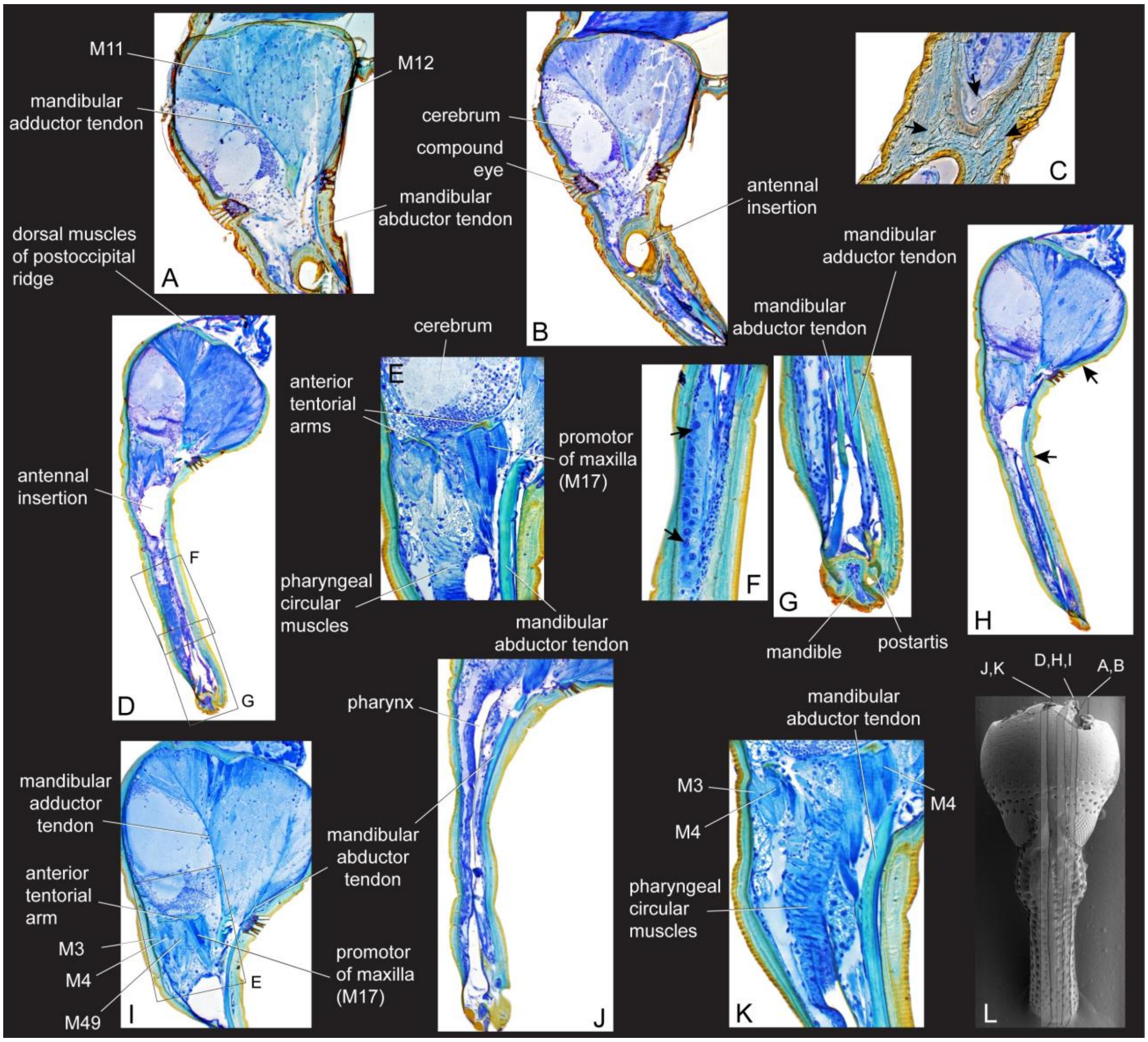
A
B
antenna
rostrum
clypeus
mandible
labrum
C
D
antenna
rostrum
clypeus
labrum
mandible
E
F
vertical setae
postantennal setae
rostrum
antenna
mandible
G
H
pronotum
legs
elytron
hind wing
pseudo-cercus
eye
rostrum
mandible
antenna
I
J
legs
elytron
antenna
hind wing
vertical setae
postantennal setae
eye
rostrum
mandible
K
pronotum
rostrum
elytron
hind wing
pseudo-cercus



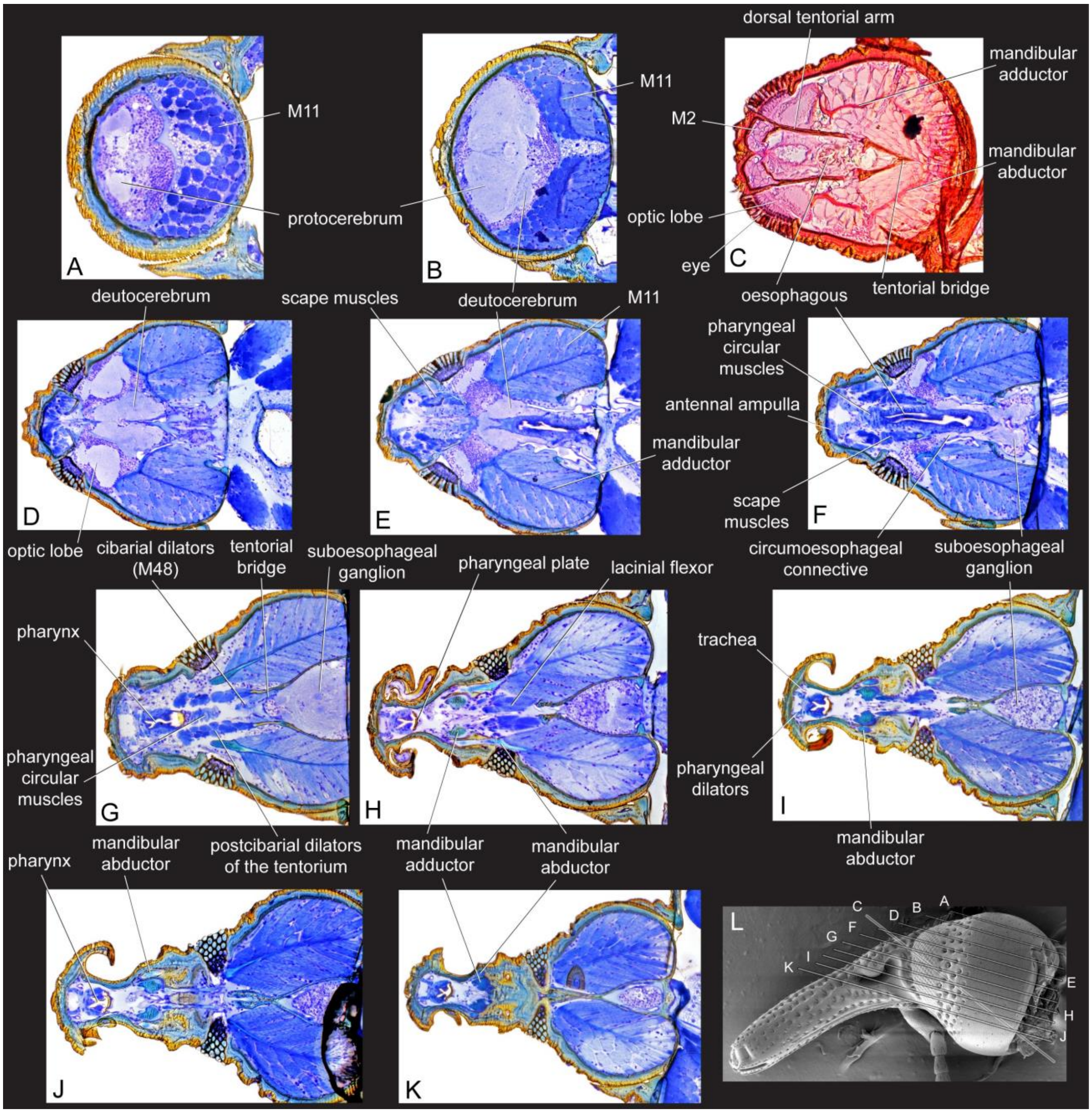
cerebrum
oesophagous
proventriculus
suboesophageal ganglion
pharynx
pupal cuticle
gastric caecum
mandible
maxilla
A
B
C
D
eye
antennal socket
rostrum
crop
salivary glands
maxilla remotor + promotor tendons
mandible
cerebrum
suboesophageal ganglion
pharynx
thoracic spiracle
proventriculus
E
F
G
G
H
postartis
mandible
postcoila
mandibular abductor
thoracic spiracle
optic lobe
maxilla
mandible
maxillary palpus
E
I,L
F
H
C
B
A
I
J
K
L
M



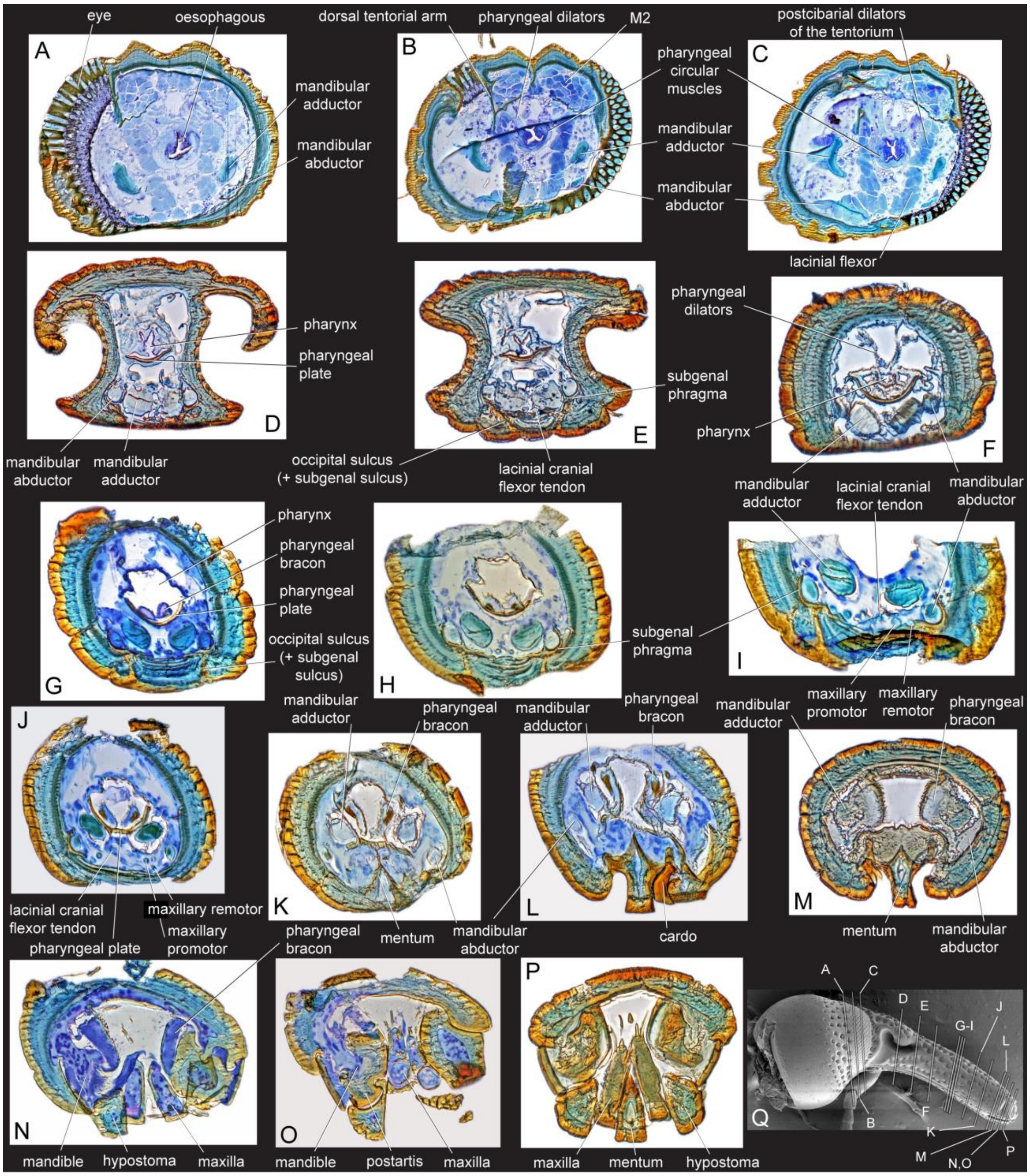
protocerebrum
optic lobe
deutocerebrum
M11
posterior tentorial arms
A
optic lobe
trachea
epidermis
cuticle
D
lipid droplet
M11
C
B
suboesophageal ganglion
posterior tentorial arms
eye
stomodaeum (oesophagous)
mandibular adductor (M11)
M12
tentorium
E
eye
F
pharyngeal dilators
mandibular adductor
mandibular abductor
G
ampullar ostium
antennal ampulla
stomodaeum (pharynx)
pharyngeal circular muscles
H
I
pharyngeal dilators
lacinial cranial flexor tendon
maxillary remotor tendon
J
maxillary promotor tendon
labial nerve
procurrent nerve
pharyngeal plate
tracheae
pharyngeal connective muscle
K
L
occipital sulcus (+ subgenal sulcus)
maxillary remotor tendon
labial nerve
maxillary promotor tendon
lacinial cranial flexor tendon
old pupal pharyngeal cuticle
pharyngeal bracon
mandibular abductor
mandibular adductor
M
N



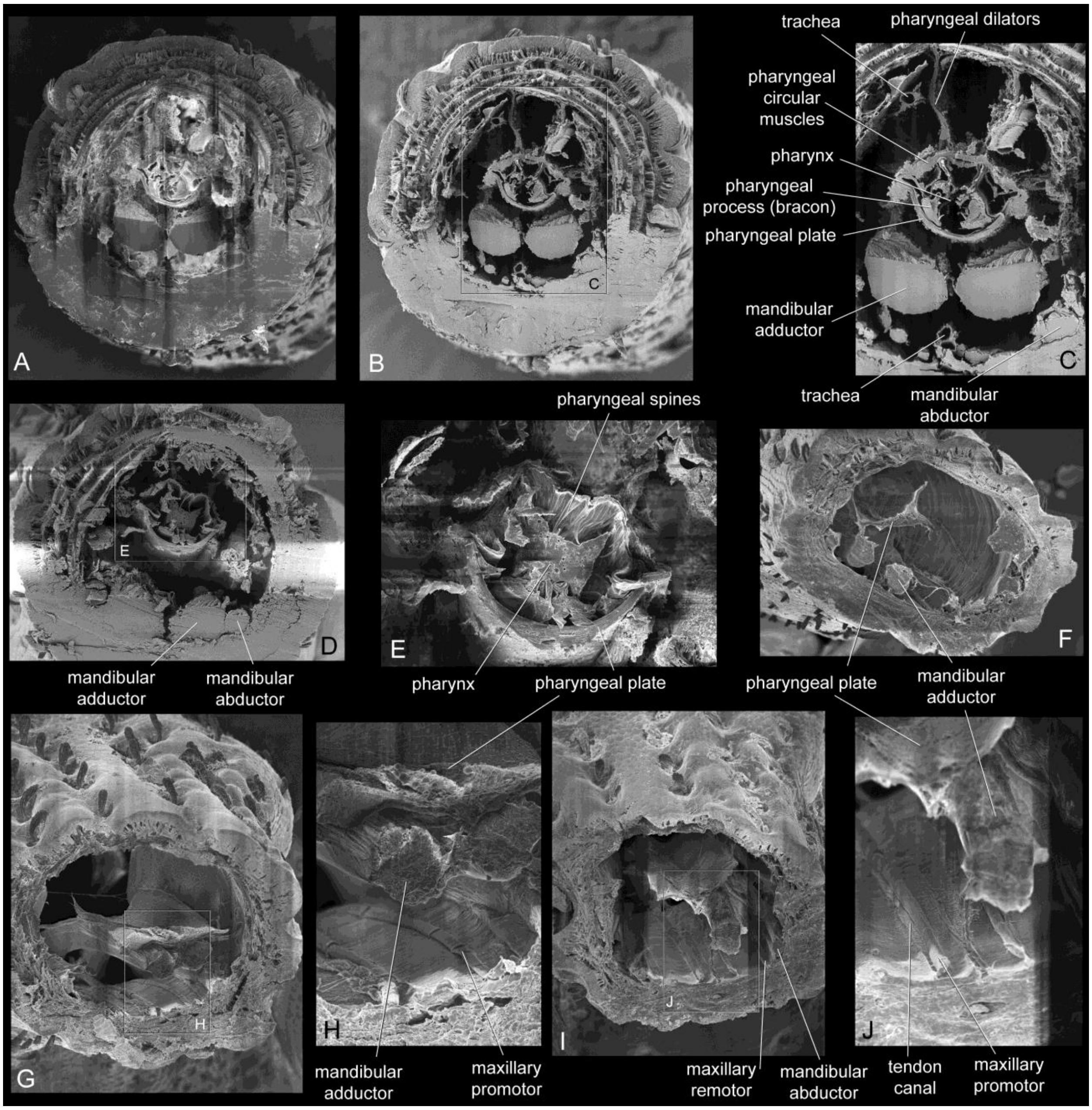
M11
M12
mandibular adductor tendon
mandibular abductor tendon
dorsal muscles of postoccipital ridge
A
cerebrum
compound eye
antennal insertion
B
C
mandibular adductor tendon
mandibular abductor tendon
antennal insertion
F
G
D
cerebrum
anterior tentorial arms
E
promotor of maxilla (M17)
pharyngeal circular muscles
mandibular abductor tendon
F
G
mandible
postartis
H
J,K
D,H,I
A,B
mandibular adductor tendon
anterior tentorial arm
M3
M4
M49
I
E
mandibular abductor tendon
promotor of maxilla (M17)
pharynx
J
mandibular abductor tendon
M3
M4
M4
pharyngeal circular muscles
K
L

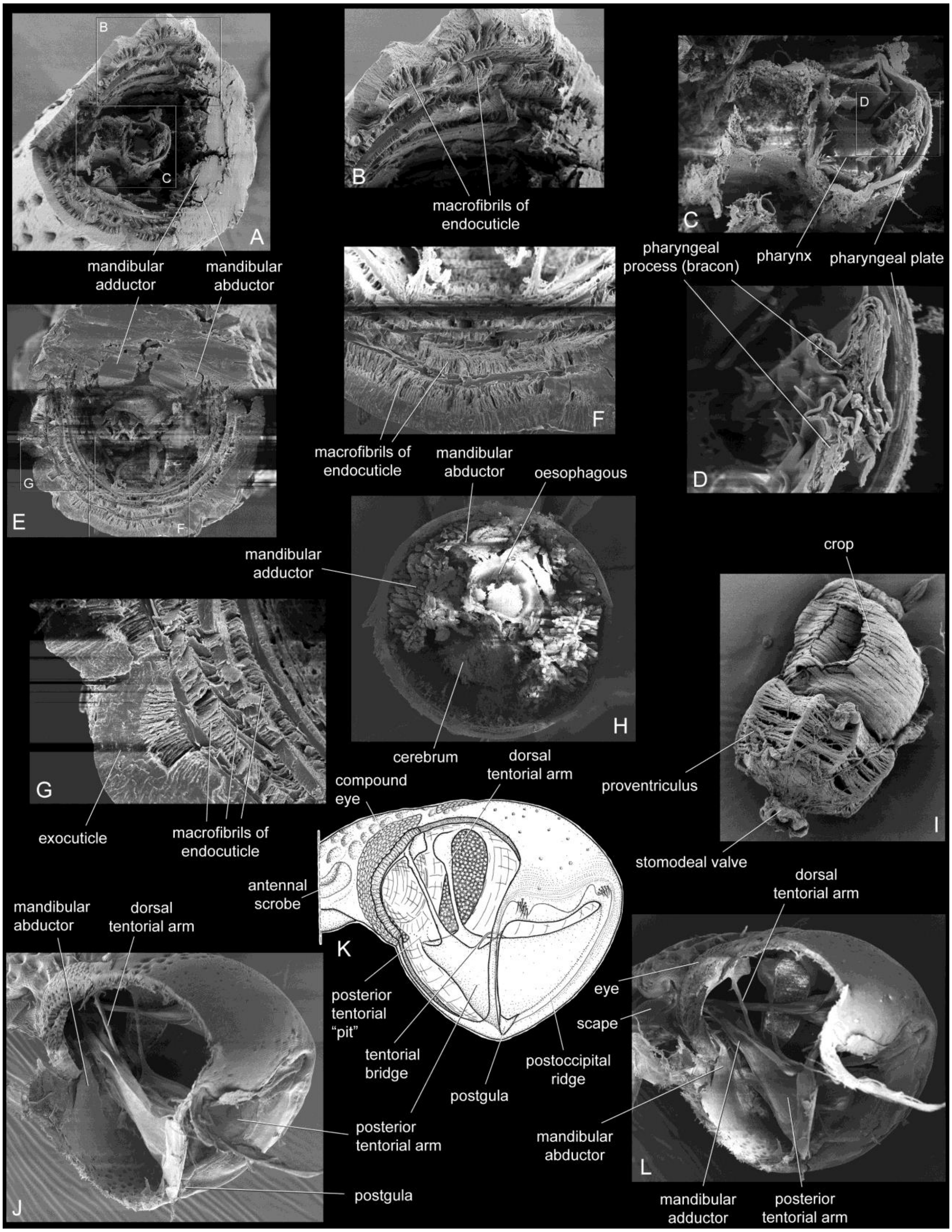


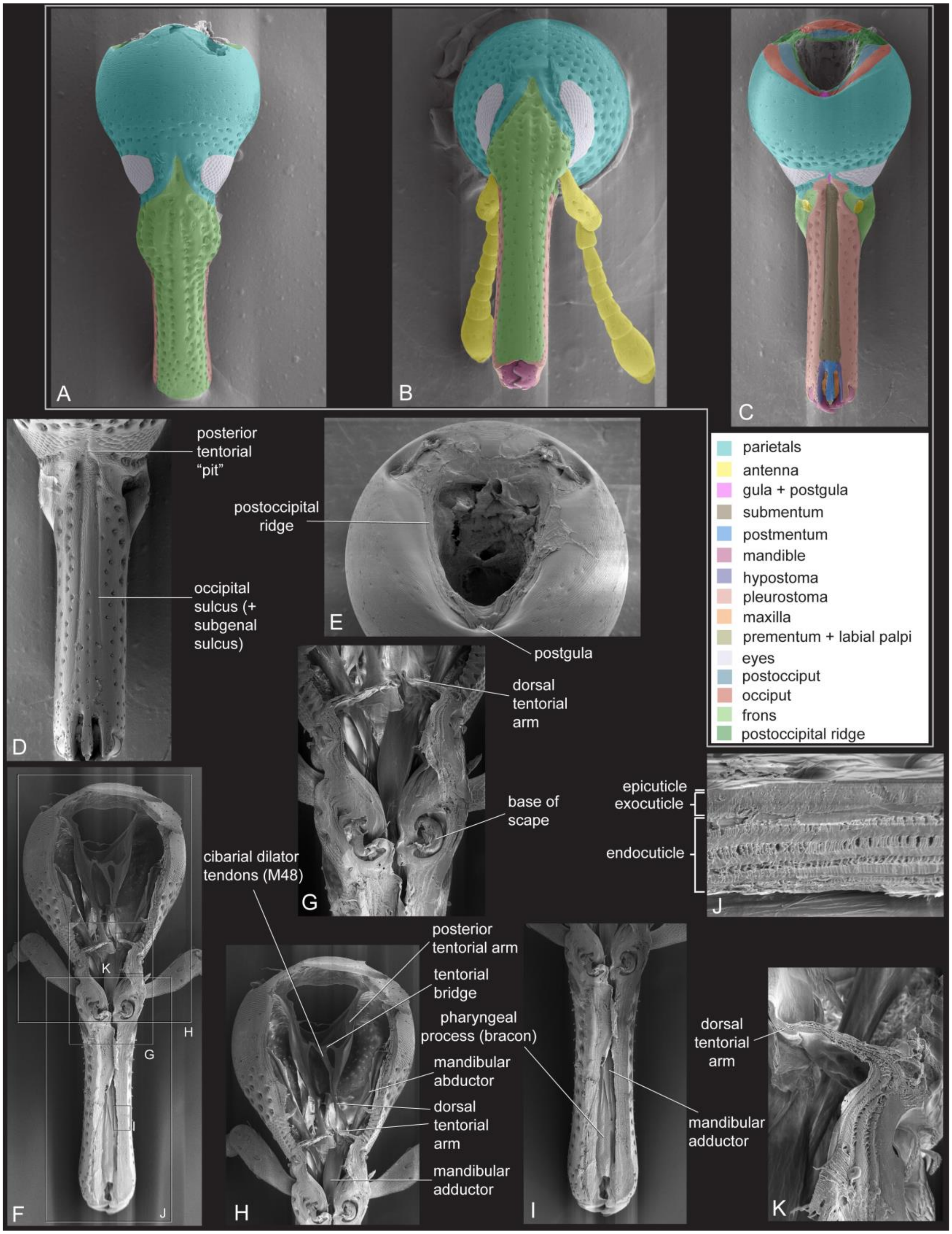
M11
protocerebrum
A
M11
B
dorsal tentorial arm
mandibular adductor
M2
mandibular abductor
optic lobe
eye
C
oesophagous
tentorial bridge
deutocerebrum
scape muscles
deutocerebrum
M11
pharyngeal circular muscles
antennal ampulla
mandibular adductor
scape muscles
D
E
F
optic lobe
cibarial dilators (M48)
tentorial bridge
suboesophageal ganglion
pharyngeal plate
lacinial flexor
circumoesophageal connective
suboesophageal ganglion
pharynx
trachea
pharyngeal circular muscles
pharyngeal dilators
G
H
I
mandibular adductor
mandibular abductor
mandibular abductor
postcibarial dilators of the tentorium
mandibular adductor
mandibular abductor
pharynx
J
K
L



A
eye
oesophagous
mandibular adductor
mandibular abductor
B
dorsal tentorial arm
pharyngeal dilators
M2
pharyngeal circular muscles
mandibular adductor
mandibular abductor
C
postcibarial dilators of the tentorium
lacinial flexor
D
pharynx
pharyngeal plate
mandibular abductor
mandibular adductor
E
subgenal phragma
occipital sulcus (+ subgenal sulcus)
lacinial cranial flexor tendon
F
pharyngeal dilators
pharynx
mandibular adductor
lacinial cranial flexor tendon
mandibular abductor
G
pharynx
pharyngeal bracon
pharyngeal plate
occipital sulcus (+ subgenal sulcus)
H
subgenal phragma
I
maxillary promotor
maxillary remotor
J
lacinial cranial flexor tendon
maxillary remotor
maxillary promotor
pharyngeal plate
K
mandibular adductor
pharyngeal bracon
mentum
mandibular abductor
L
mandibular adductor
pharyngeal bracon
cardo
M
mandibular adductor
pharyngeal bracon
mentum
mandibular abductor
N
pharyngeal bracon
mandible
hypostoma
maxilla
O
mandible
postartis
maxilla
P
maxilla
mentum
hypostoma
Q
A
C
D
E
G-I
J
L
B
F
K
M
N,O
P


trachea
pharyngeal dilators
pharyngeal circular muscles
pharynx
pharyngeal process (bracon)
pharyngeal plate
mandibular adductor
trachea
mandibular abductor
A
B
C
pharyngeal spines
D
E
F
mandibular adductor
mandibular abductor
pharynx
pharyngeal plate
pharyngeal plate
mandibular adductor
G
H
I
J
mandibular adductor
maxillary promotor
maxillary remotor
mandibular abductor
tendon canal
maxillary promotor


B
C
A
macrofibrils of endocuticle
D
pharyngeal process (bracon)
pharynx
pharyngeal plate
mandibular adductor
mandibular abductor
G
E
F
macrofibrils of endocuticle
mandibular abductor
oesophagous
D
mandibular adductor
crop
H
G
cerebrum
dorsal tentorial arm
compound eye
proventriculus
exocuticle
macrofibrils of endocuticle
I
stomodeal valve
antennal scrobe
dorsal tentorial arm
mandibular abductor
dorsal tentorial arm
K
posterior tentorial "pit"
eye
scape
tentorial bridge
postoccipital ridge
postgula
posterior tentorial arm
mandibular abductor
L
J
postgula
mandibular adductor
posterior tentorial arm


A
B
C
parietals
antenna
gula + postgula
submentum
postmentum
mandible
hypostoma
pleurostoma
maxilla
prementum + labial palpi
eyes
postocciput
occiput
frons
postoccipital ridge
posterior
tentorial
"pit"
occipital
sulcus (+
subgenal
sulcus)
D
postoccipital
ridge
E
postgula
dorsal
tentorial
arm
base of
scape
G
epicuticle
exocuticle
endocuticle
J
cibarial dilator
tendons (M48)
K
H
G
I
J
F
posterior
tentorial arm
tentorial
bridge
pharyngeal
process (bracon)
mandibular
abductor
dorsal
tentorial
arm
mandibular
adductor
H
I
mandibular
adductor
dorsal
tentorial
arm
K

## 5. The weevil rostrum (Coleoptera: Curculionoidea): internal structure and evolutionary trends

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**Abstract**:

Weevils (Coleoptera: Curculionoidea) are one of the most diverse groups of extant organisms, with approximately 60,000 described species. They are extremely important economically, being of great agricultural significance because they are associated with all major groups of plants and plant parts. The current classification of weevils, despite having witnessed numerous hypotheses, is still quite unstable at the higher levels and even more so at the lower levels. In order to develop a more robust morphological character system for cladistic analysis of the higher lineages and to gain a comprehensive understanding of rostrum structure prior to developmental studies examining its formation, a comparative study was conducted of rostrum structure throughout Curculionoidea. Thin sections were made of the rostra of exemplar taxa representing most of the weevil families, as well as several subfamilies within the largest family, Curculionidae, and internal structures were examined for useful characters. While the morphological diversity of rostral forms is rather astounding, general trends are apparent with respect to life history traits and modes of feeding. Internal rostral morphology also represents a valuable set of previously unexplored characters; more informative than traditional external morphology, these features provide new insight into rostral morphology and have implications for settling current incongruence in the higher classification.

**Keywords:** morphology, histology, phylogeny, adult structure

## Introduction

Weevils (Coleoptera: Curculionoidea) are one of the most diverse groups of extant organisms, with approximately 60,000 described species. They are extremely important economically, being of great agricultural significance because they are associated with all major groups of plants and plant parts. The current classification of weevils, despite having witnessed numerous hypotheses, is still quite unstable at the higher levels and even more so at the lower levels. In order to develop a more robust morphological character system for cladistic analysis of the higher lineages and to gain a comprehensive understanding of rostrum structure prior to developmental studies examining its formation, a comparative study was conducted of rostrum structure throughout Curculionoidea. Thin sections were made of the rostra of exemplar taxa representing most of the weevil families, as well as several subfamilies within the largest family, Curculionidae, and internal structures were examined for useful characters. While the morphological diversity of rostral forms is rather astounding, general morphological trends are apparent. Internal rostral morphology also represents a valuable set of previously unexplored characters; similar to traditional external morphology, these features provide new insight into rostral morphology and have implications for settling current incongruence in the higher classification.

## Methods

### *Taxon sampling*

Semi-thin sections were produced for all 7 of the currently recognized, extant families within Curculionoidea, and all 10 recognized subfamilies within Curculionidae. The sampling design mostly followed Alonso-Zarazaga and Lyal (1999), with some exceptions in order to incorporate current and evolving views in the classification, but the general classification scheme followed here is that of Oberprieler *et al.* (2007). In order to have some idea of the variability of internal rostral morphology, sampling of more than one taxon was possible within the families Scolytidae, Attelabidae, and Brentidae. Within Curculionidae, sampling of more than one taxon was performed for a few subfamilies, including Dryophthorinae, Curculioninae, and Molytinae. Of course, it would be of great interest to extend this study to include a more diverse sampling, but the range covered herein is considered adequate to make many well-supported conclusions as well as further hypotheses.

### *Histological sectioning*

Weevil heads were first dehydrated in 100% ethanol. Infiltration of head tissue consisted of approximately twelve hour incubation periods through a series of 1:1 then 1:2 ethanol to LR White mixtures. Heads were placed in gelatin capsules and embedded in pure LR White (Electron Microscopy Sciences). Following thermal curing in an oven for ~24 hours at 60°C, embedded heads were removed from the capsules and sectioned using a Leica EM UC6 ultratome and diamond knife, producing semi-thin sections ~5–6 μm thick. Sections were transferred to glass slides, stained in toluidine blue, and digitally photographed with a Canon EOS-1 camera mounted on an Olympus BX51 compound microscope. Regarding most photomicrographs, a z-stack was acquired of several images, combined using the software CombineZ, and edited in Adobe Photoshop CS3.

### *Electron microscopy*

Scanning Electron Microscope (SEM) images were captured using a LEO 1550 FESEM (Field Emission Scanning Electron Microscope). Heads were mounted on SEM stubs using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite, and coating was performed using gold.

### *Phylogenetic analysis*

The morphological character matrix, consisting of 16 adult rostral characters coded for 36 taxa, was constructed in WinClada (Nixon 1999b). Parsimony analyses were performed using Nona (Goloboff 1999), in which the Ratchet search algorithm was implemented (Nixon 1999a) several times using different search configurations in order to maximize exploration of tree space and ensure convergence on a stable topology. Successive searches consisted of analyzing 8-11 characters for 500-4,000 iterations and using 2 simultaneous threads. The results presented here are based on an analysis of 11 characters for 1,000 ratchet iterations using 2 simultaneous threads.

## **Results**

### *Character list*

Morphological characters of this study were largely restricted to the rostrum, specifically to the post-ocular region, and to features visible in semi-thin sections. While other features of the head are certainly of great phylogenetic utility, such features already have been well-studied, particularly by Morimoto and Kojima (2003) and Morimoto *et al.* (2006).

Below is a list of the characters scored in this study. Of the morphological variation observed in internal rostrum structure throughout Curculionoidea, the most significant features appear to include the ventral sulci and their associated apodemes, and the tendons of the mouthparts, particularly in the nature by which the mandibular and maxillary tendons are positioned and held by the apodemes. As no suitable outgroup possesses a developed rostrum (which potentially could cause difficulty in character polarization if included), Nemonychidae was used to root the tree.

1. Apodemes of occipital and subgenal sulci: (0) both supporting tendons; (1) only apodemes of occipital sulci supporting tendons (those of the subgenal sulci reduced/absent).

As both pairs of sulci (occipital and subgenal) are fairly visible externally and present in basal Curculionoidea, their associated internal apodemes support the mandibular and maxillary tendons. Towards the higher weevils, the subgenal sulci disappear and the occipital sulci then assume the role of supporting these pairs of tendons. Lyal (1995) speculated that in the higher weevils where the subgenal sulci are absent, the sulci and their apodemes may have been incorporated into the bridge that is formed from the medial fusion of the apodemes of the occipital sulci in several lineages. This hypothesis may be plausible, as is seen by the relative positions of the maxillary tendons in the lineages bearing these two discernible forms; however, it is also possible that the subgenal sulci, along with their associated apodemes, were simply lost entirely as the occipital sulci migrated ventro-medially.

2. Apodemes of occipital and subgenal sulci at approximate middle of rostrum: (0) remaining separate; (1) becoming fused internally; (2) subgenal sulcus absent.

Beginning from the oral area and proceeding towards the base of the rostrum, the occipital and subgenal sulci (as determined by the invagination of the exocuticle) are separate and may remain completely separated or fuse to varying degrees. Just as these sulci may remain separated or possibly have become fused, their invaginated apodemes may also remain separated or become fused internally in the rostrum. Separate sulci often denote separate apodemes for supporting the mouthpart tendons (*i.e.*, in Nemonychidae), but these apodemes also show the trend of becoming fused (such as in Attelabidae).

3. Apodemes of occipital sulci: (0) separate; (1) becoming fused medially; (2) fused and stalked medially.

Of the lineages that possess a single pair of ventral rostral sulci (occipital), which may represent a fusion of the occipital and subgenal sulci, their apodemes may remain separate or subsequently fuse to form a medial bridge. As mentioned above, it has been hypothesized (Lyal 1995) that this medial bridge represents the fused apodemes of the subgenal sulci, in which case these apodemes would not be lost but merely subsumed into the internal scaffold created by the apodemes. It is also possible that the subgenal sulci and its associated apodeme are lost, in which the medial fusion of these apodemes are purely an extension of the occipital apodemes.

4. Apodeme and tendon orientation (in lineages where the occipital and subgenal apodemes are fused): (0) apodemes stratified horizontally, mandibular adductor tendons situated outside of abductor tendons; (1) apodemes stratified horizontally, mandibular abductor tendons situated

outside of adductor tendons; (2) apodemes stratified vertically, mandibular adductor tendons situated above abductor tendons; (3) apodemes stratified laterally (mandibular adductor tendons situated at a level lower than that of abductor tendons).

In all cases where the occipital and subgenal sulci remain separate, the occipital apodemes are situated in the ventro-lateral corners of the rostrum and the subgenal apodemes are situated approximately ventro-medially in the rostrum. In lineages where the subgenal sulci are absent and only the occipital are present, apodeme structure differentiates along two apparent paths. When only the occipital sulci are present, its apodemes are located ventro-medially and are often stratified horizontally, in which an outer canal supports the mandibular abductor tendon and an inner canal/broadly concave surface supports the adductor tendon and maxillary tendons. Another condition is having the same general layout of the tendons, but in which the sulci are located ventro-laterally, causing the apodemes supporting the mandibular abductors to be at a level higher than those supporting the mandibular adductors and maxillary tendons. This condition is expressed as having the tendons stratified laterally. It seems to nearly represent a similar condition to that of the horizontal stratification, but appears to show ample consistency to maintain a separate state. From these conditions above, the apodemes may become fused, forming a medial bridge that remains stratified horizontally or that becomes stratified vertically. In this latter condition, the inner arm of the apodeme supporting the abductor tendon extends further to enclose the tendon in a ventral tunnel on the floor of the rostrum, the adductor tendon then assumes a position above the abductor tendon.

5. Apodemes of postmentum: (0) free/separated basally; (1) fused medially; (2) fused and stalked medially.

This pair of apodemes arise from the postmentum (and to some degree may also arise from the hypostomal-labial sulci) and form a scaffold to support the anterior portions of the pharynx, pharyngeal plate, and mandibular adductor tendons. In many lineages it also forms somewhat of an X-shaped scaffold, in which the apodemes may remain separated (typically when also weakly developed) or may fuse medially to various degrees. Fusion occurs by which a medial bridge joins the two apodemes or by the two apodemes joining more completely medially and forming a stalk. Typically, the apodemes are rather weakly-developed when separate, often only composed of endocuticle, and become stronger, more well-developed when the apodemes fuse and incorporate more exocuticle.

6. Apodemes of postmentum, canals supporting adductor tendons: (0) weakly developed, lacking exocuticle; (1) strongly developed with exocuticle.

As noted above, the apodemes of the postmentum often are weakly-developed when separate and more strongly-developed when fused medially. In the former condition, the dorsal extensions of these apodemes support the mandibular adductor tendons at their distal reach near the oral orifice and form a shallowly concave shelf for the tendons. In the strongly-developed condition, these dorsal extensions form a distinct and sturdy canal for the adductor tendons.

7. Anterior of occipital sulcus (adjacent to posterior mandibular articulation): (0) elongated and continuous to eyes, supporting mandibular abductor tendons; (1) short, abrupt, disjunct from posterior part of sulcus.

At the anterior extension of the occipital sulcus, it joins the subgenal sulcus just posterior to the posterior mandibular articulation. In lineages that retain distinct and separate occipital sulci along the length of the rostrum, it can be traced as a (mostly) continuous line that runs from the ventral margin of the compound eyes, near the base of the rostrum and gradually extends slightly laterally towards the rostral apex, in which its apodemes support the abductor tendons. In lineages in which the subgenal sulci are absent, the anterior extension of the occipital sulcus is still visible, but it is abrupt, quickly disappearing just posterior of the mandibles and towards the rostral base.

8. Position of maxillary tendons near oral orifice (pre-antenna): (0) supported by lateral canals of the postmental apodemes; (1) at least one supported in the inner angle of the postmental apodemes; (2) not supported by apodemes.

The three tendons that originate from the maxilla are the maxillary remotor, promotor, and lacinial cranial flexor tendons. Generally, three arrangements of these tendons are visible in the area near the oral orifice in which the apodemes of the postmentum are still present. In most basal lineages of Curculionoidea there are small lateral canals stemming from the apodemes of the postmentum which support the maxillary tendons, though not all necessarily are supported. In many lineages, often where the apodemes of the postmentum form approximate right to subacute angles below the pharynx, one tendon may be supported in that inner angle. In the third condition the tendons may not be supported by any apodemes.

9. Postition of mandibular abductor and adductor tendons: (0) abductor and adductor tendons supported by/resting on apodemes; (1) abductor tendons supported by apodemes, adductor tendons not supported by/resting on apodemes.

The mandibular tendons usually are supported by apodemes of the ventral sulci of the rostrum in weevils. This condition typically varies in lineages where the rostrum is short to nearly absent, though there are exceptions. In these cases, while the abductor tendons always are supported by an apodeme (with the possible exception of some Scolytidae and Platypodidae), the adductor tendons may remain suspended above the ventral floor of the rostrum when the rostrum is short to nearly absent.

10. Hypostomal-labial sulcus: (0) fully developed, extended, connecting to subgenal sulci; (1) partially/weakly developed, abbreviated.

The pair of sulci that extend from near the base of the postmentum, posterior to the pleurostomal sinus, was termed the hypostomal-labial sulci by Lyal (1995). All weevils appear to possess this sulcus in various degrees of development. A fully developed sulcus, which generally is fairly elongate and apparently extends to the subgenal sulcus (hypostomal sulcus), is present in several basal lineages and appears to contribute (along with the postmentum) to two pairs of apodemes: one medial pair, which is less developed and generally smaller in the more primitive weevil lineages, and one lateral pair that extends laterally and fuses with the apodemes produced from the anterior end of the occipital sulci. A partially-developed or weakly-developed sulcus is present in the more derived weevil lineages. This condition is characterized by a sulcus which is short and disjunct from the subgenal sulci or often not clearly discernable externally. In the weakly developed condition there also appears to be just one pair of apodemes (the medial pair) that extend from the sulci, in which the laterally produced pair have been greatly reduced or lost. This medial pair of apodemes is much more robust in the more derived lineages, contributing to a strong C-shaped canal for the mandibular adductor tendons.

11. Pharyngeal plate immediately after middle of rostrum (apicad): (0) weak, incompletely developed/sclerotized, exocuticle at most on lateral portions; (1) fully developed, completely sclerotized with exocuticle.

All weevils, or at least the majority, possess a chitinous pharyngeal plate that supports the pharynx and ends before the beginning of the oesophagous. The anterior extension of the pharyngeal plate near the oral orifice is associated with the apodemes of the postmentum and hypostomal-labial sulci and produces lateral ramifications that form canals to hold the mandibular adductor tendons for a short distance. In the lineages with a distinguishable rostrum, the pharyngeal plate appears strongly sclerotized and composed of exocuticle; however, in those possessing a shortened rostrum, the plate often is weakly sclerotized, appearing almost absent, and is largely composed of endocuticle.

12. Position of maxillary tendons (3) on apodemes (at approximate middle of rostrum): (0) 2 central tendons, 1 positioned laterally under adductor tendon; (1) 3 central tendons; (2) 1 central tendon, 2 lateral (1 positioned under and 1 positioned above adductor tendon); (3) 2 central tendons, 1 positioned laterally above adductor tendon.

Depending on the orientation of the maxilla (and other mouthparts), the tendons of the maxilla may also reflect these different orientations. Upon examination of cross sections of the rostrum, the following conditions have been observed. There may be two central tendons (the maxillary promotor and lacinial cranial flexor tendons) and one lateral tendon (the maxillary remotor) positioned underneath the mandibular adductor tendon; all three tendons may be positioned centrally; there may be one central tendon (the maxillary promotor) and two lateral tendons, one (the maxillary remotor) positioned underneath the mandibular adductor tendon and the other (lacinial cranial flexor tendon) positioned above the adductor tendon; or there may be two central tendons (the maxillary promotor and remotor tendons) and one lateral tendon (the lacinial cranial flexor tendon) positioned above the mandibular adductor tendon.

13. Anterior extension of subgenal sulcus (*i.e.* pleurostomal sulcus at anterior mandibular articulation): (0) present; (1) absent.

In several of the basal weevil lineages, the antero-dorsal extension of the pleurostomal sulcus is present (although generally not visible externally). Ancestrally, this sulcus is the part of the subgenal sulcus just posterior to the mandibles and connects to the anterior tentorial pits posterior to the anterior mandibular articulation. In the more derived lineages (essentially in Curculionidae), the pleurostomal sulcus has been lost.

14. Remnant of anterior tentorial arms: (0) present; (1) absent.

Although Morimoto and Kojima (2003) state that the anterior tentorial arms have disappeared in all Curculionoidea excepting Belidae (in which they observed remnants at the base of the tentorium), the current study reveals that remanants of the anterior arms are present throughout the superfamily. Due to difficulty in finding the small portions of these arms, this feature has remained elusive in weevils for some time, though it is possible to view them in SEM images, semi-thin sections, and specimens in which the cuticle has been cleared. Ting (1936) illustrated the anterior arms in *Ithycerus*, *Rhynchites*, and *Platypus*, though did not discuss the distribution of their presence throughout the superfamily.

15. Gular (postoccipital) sutures: (0) separate, paired; (1) fused medially.

Only a few groups (i.e., Nemonychidae, Anthribidae, and Belidae) have discernible gular regions delimited by separate gular sutures. In the remainder of the superfamily, the gula has been lost due to the reduction of the gular region by the medial fusion of the gular sutures. It has been reported by Wood (1986) that a gula is present in some scolytids, namely in some species of *Gnathotrupes*. While it certainly is possible that some Scolytidae possess remnants of a gula, especially if this group arose contemporaneously with the other basal families, this observation has yet to be affirmed. In many cases, an enlarged postgular area may be hypothesized as the remnant of a gula. Lyal (1995) hypothesized that the postgula represents a fusion of the cervical sclerites to the margin of the occipital foramen. This observation is interesting, particularly given the bilobed shape of the postgula in many taxa. In several cases, however, a remnant of separate cervical sclerites is visible, both in basal and more derived Curculionoidea.

16. Labrum: (0) present; (1) absent, fused with frons.

A distinct, articulating labrum is present only in Nemonychidae and Anthribidae. Wood (1986) mentions that many lineages within Scolytidae and Platypodidae have an enlarged epistomal lobe (though the same might be said of many Attelabidae as well) which appears to be demarcated in several taxa and even delimited by a rudimentary sulcus.

*Phylogeny utilizing rostral characters*

The strict consensus tree of 1476 most-parsimonious trees, L= 112, Ci=19, Ri=35 (MP trees of L=55, Ci=40, Ri=76) is presented in presented in figure 1, mapping both characters reconstructed with an accelerated optimization (Fig. 1A) and delayed optimization (Fig. 1B).

This phylogeny demonstrates that in internal characters of the rostrum examined in this study may be of greatest utility at approximately the family level. By examining the 50% majority rules tree (L=65, Ci=33, Ri=69), it appears that the rostral characters are quite informative, and perhaps with a larger taxon sampling, more information may be obtained, particularly within the Curculionidae.

*General and internal anatomy of the adult weevil rostrum*

Preceeding descriptions of the internal structure of the rostrum throughout Curculionoidea, as viewed through histological sections, it is critical to outline the general features (mostly sclerotized) that are present and their characteristics as seen in semi-thin cross-sections (Fig. 3).

Beginning at the anterior apex of the rostrum and sectioning through the mouthparts, a few differences are readily visible regarding their orientation. As documented by Morimoto (1981) and Morimoto and Kojima (2003), there are differences in which the mouthparts are angled throughout Curculionoidea. While the more primitive lineages appear to have mandibles that act in the horizontal plane, moving towards more derived lineages, this plane shifts more obliquely and nearly vertically in several groups. This rotational shift also is visible in the orientation of the mandibular articulations, namely the position of the anterior condyle and the posterior acetabulum on the rostrum. Along with the change in the positions of these points of articulation, it is largely the size proportions of other features that accompany this fundamental orientation of the mouthparts. For example, most noticeable of these changes is the reduction in the mandibular adductor tendons and the enlargement of its abductor tendons. This shift in tendon size indicates a different mode of action of the mandibles; the shift from a chewing action to one of a more rasping or scraping nature.

Plesiomorphically in insects, it is possible to divide the subgenal sulcus into two distinct parts in order to more clearly delineate cranial regions (Snodgrass 1935). The pleurostomal sulcus, comprising the anterior-most section of the subgenal sulcus, runs just behind the mandible. It connects to the anterior tentorial pits, which are also just posterior to the anterior mandibular articulation, and eventually merges with the occipital sulcus (close to the posterior mandibular articulation). The hypostomal sulcus continues from where the pleurostomal sulcus joins the occipital sulcus, ending at the posterior tentorial pits (from which the gular sutures [postoccipital sutures] continue in Coleoptera). In Curculionoidea, the anterior tentorial pits are difficult to locate externally; however, remnants of the anterior tentorial arms usually are visible in sections (Figs. 6, 7, 11, 12, 15, 16) and are occasionally visible after dissection in the majority of Curculionoidea (Fig. 10), though they do not extend very far posteriorly. Proceeding further from the base of the weevil phylogeny, these arms may disappear within some tribal lineages of Curculionidae, though in depth discussion of such reduction is not possible from this study alone. Although Morimoto and Kojima (2003) mention that the anterior tentorial arms seem to be obliterated in all weevils excepting Belidae (which also possess remnant bases of the arms), it has become apparent in this study that at least a small anterior portion of the arms (where they attach adjacent to the dorsal mandibular articulation) are present throughout the superfamily, often being more noticeable in several basal families, including Scolytidae and Platypodidae. Near the anterior mandibular articulation, the pleurostomal sulcus is visible in several basal families as an invagination of the exocuticle (as are all sulci) and it is lost beginning in the Dryophthoridae.

An interesting modification of the ventral head sulci arises in Coleoptera that involves the hypostomal sulcus and includes a novel sulcus, the hypostomal-labial sulcus, which appears to separate the hypostoma from submentum (Lyal 1995). While the hypostoma reaches the posterior extension of the submentum (and the posterior tentorial pits) in other insects, it shifts anteriad in Coleoptera, thereby elongating the hypostomal sulcus and essentially extending the postgena to also unite with the submentum (in addition to the posterior extension of the submentum fusing with the gula). Due to the formation of the rostrum in weevils, while remnants of the pleurostomal sulcus are visible, the hypostomal sulcus is for the most part indistinguishable, apparently excepting some Scolytidae and Platypodidae (Figs. 15-16). The separations of the pleurostomal + genal regions and the hypostomal + postgenal regions in weevils, then, become somewhat ambiguous due to the loss of sulci that are used to delimit these regions. Beginning with Belidae, Ithyceridae, and Brentidae, and continuing throughout the higher Curculionoidea, the situation becomes further complicated with the apparent merging of the hypostomal and occipital sulci, thereby eliminating most or all of the hypostomal + postgenal region. This fusion leaves various possibilities as seen in higher Curculionoidea (beyond the three groups just mentioned above) involving a pleural region of the rostrum composed partially of the frons (in which the antennae can be found in numerous positions along the rostrum) and partially of the pleurostoma + genal region of the parietals (Davis 2011).

The hypostomal-labial sulcus appears to be present in all weevils. Generally, this pair of sulci are nearly indiscernible externally (excepting most Scolytidae and Platypodidae) and barely detectable in semi-thin sections, rather short in the basal weevils and greatly abbreviated in the higher weevils. Posteriad are two pairs of sulci, the subgenal and occipital sulci. While the plesiomorphic state of separate subgenal and occipital sulci is observed in Nemonychidae, some

Anthribidae, and Attelabidae, the remainder of Curculionoidea essentially only possess one pair of ventral sulci. It is possible that, over the course of time, the subgenal sulci became fused with or were subsumed into the occipital sulci, particularly given the extensive apodemes that form from this pair of sulci in the higher weevils. It is also plausible, however, that the subgenal sulci simply were lost as the occipital sulci migrated medio-ventrally, thus those that remain are the occipital sulci that support not only the mandibular adductor tendons, but also the adductor tendons and those of the maxilla.

In most extant Curculionoidea, in which the rostrum is fairly curved, most mouthpart tendons are situated in cuticular canals that guide and facilitate their sliding action (Fig. 3). The canals for the larger mandibular tendons, naturally, are quite deep, and constitute apodemes formed by the occipital sulci. In weevils that possess distinct subgenal sulci, separate apodemes are present for supporting the maxillary tendons. In most higher weevils, such as Curculionidae, where only the occipital sulci are present, the apodemes of the sulci have formed a medial bridge. The tendons of the maxilla, then, rest in canals on this bridge. Nearing attachment to the mouthparts, as was the case at the base of the rostrum, the tendons take a more central position in the rostral cavity, eventually arriving adjacent to and partially enclosed by the pharyngeal bracons. Also at the apex, the pharynx widens, the pharyngeal bracons become more visible, and the apodemes of the submentum and hypostomal-labial sulci, which facilitate in supporting the mandibular adductor tendons, are visible.

*Internal rostrum structure throughout Curculionoidea*

<u>Outgroups (Figs. 4-5)</u>:

Outside of Curculionoidea, the ventral head sulci do not invaginate to produce apodemes as they do in weevils. The pharyngeal plate tends to be more sclerotized (if it is present at all) in lineages with some derivation of a rostrate head. As weevils bear the most developed and longest rostra, they have developed relatively robust pharyngeal plates to support the pharynx along its extended length. While rostra have developed in some other coleopteran lineages (e.g., Lycidae, Salpingidae (Fig. 4), Staphylinidae), weevils appear to have uniquely derived the apodemes of the ventral head sulci used to support the mouthpart tendons, as such apodemes and invaginations of the exocuticle or endocuticle are absent in these other families (e.g., Chrysomelidae; Fig. 5).

<u>Nemonychidae (Fig. 6)</u>:

Although Nemonychidae are known to be at the very base of Curculionoidea, the extant fauna (as with all of the extant weevil groups) appears to show a somewhat derived rostral form. As Lyal (1995) clearly illustrated, a hypothesized weevil ancestor or early weevil lineage would probably display all sutures and sulci on the head, including distinctly separate subgenal and occipital sulci. While the study herein examined only one nemonychid representative, its features do not appear as primitive as had been suspected. If one could clearly visualize the head features of some of the extinct nemonychid lineages, it is probable that more primitive features showing closer resemblance to the hypothesized weevil ancestor of Lyal's would be found. In extant Nemonychidae, the plurostomal sulcus is visible in cross-section as a somewhat lateral line extending from near the anterior mandibular articulation. Remnants of the anterior tentorial arms are also visible as a pair of small circles of exocuticle near the dorso-lateral corner of the rostrum, just posterior to the mandibles. The subgenal and occipital sulci appear to be separate, though

Anthribidae (Figs. 7-8):

Anthribidae show a form similar to that of Nemonychidae, particularly in reference to the position of the occipital and subgenal sulci. The enlarged, bilobed postmentum is a rather striking feature of this family and contributes to the well-developed scaffold formed from the apodemes of the hypostomal-labial sulci, similar to what is present in Attelabidae. The pleurostomal sulci are distinct.

Belidae (Fig. 9):

The occipital apodemes are present, supporting all of the mouthpart tendons, and the subgenal apodemes appear to have been lost. A peculiar feature of the belid rostrum lies in the arrangement of the mandibular tendons. The adductor tendons nearly always are situated mesially in the rostrum with the abductor tendons more lateral, thereby positioned along the rostrum according to their point of derivation from the mandible. While the positions of these tendons are normal along the anterior portion of the rostrum, they change position posterior to the antennae, in which the adductor tendons assume the more lateral position in the apodemes of the occipital sulci. The apodemes of the hypostomal-labial sulci are simple and rather elongate dorsally. The pleurostomal sulci also are distinct.

Attelabidae (Figs. 10-12):

*Attelabinae* (Figs. 10-11): This group possesses separate occipital and subgenal sulci, though the latter (and the associated apodemes) may be reduced in short snouted taxa. As in Anthribidae, the apodemes of the hypostomal-labial sulci are fairly elaborate. The pleurostomal sulci are distinct.

*Rhynchitinae* (Fig. 12): Similar to Attelabinae, both the occipital and subgenal sulci are distinctly separate and bear well-developed apodemes. While these pairs of sulci remain separate along the length of the rostrum, their apodemes fuse on each side and form a bridge. The pleurostomal sulci are distinct.

<u>Scolytidae (Figs. 13-15)</u>:

*Scolytinae* (Figs. 13-14): As the rostrum in the extant members of this group is more or less absent, with only remnants present in some taxa, much information has been lost in terms of sulci and tendon position, as well as degree of apodeme development. As the rostrum mostly has been lost, internally it appears rather similar to that of a chrysomelid, in which tendons do not require supporting apodemes to facilitate movement and reduce damage. The occipital sulci, therefore, are fairly short, their apodemes also being short and appressed along the rostrum wall. The pleurostomal sulci appear to be absent in this subfamily.

*Hylesininae* (Fig. 15): Hylesininae is thought to be the more basal group within this family and, in accordance with this hypothesis, it indeed displays more primitive features as seen in sections. While the subgenal sulci appear to largely be absent in Scolytinae, they are comparatively distinct in Hylesininae. The apodemes of the occipital sulci also are slightly more developed and not as appressed to the rostrum wall. The pleurostomal sulci are distinct.

Platypodidae (Fig. 16):

This groups appears more similar to Scolytinae in internal rostrum structure, though the occipital sulci are rather indistinct. While there seems to be a faint line of exocuticle near the dorsal mandibular articulation, distinct pleurostomal sulci are not evident.

Caridae (Fig. 17):

In Caridae the pleurostomal region extends more ventral than in all other weevils, a feature noticeable by the ventral insertion of the antennae. As such, the occipital sulci have also migrated ventrally and nearly touch mesially. This character is visible in sections whereby the sulci are adjacent, causing the tendons to be located fairly closely as well. The pleurostomal sulci also are distinct.

Ithyceridae (Fig. 18):

The middle part of the rostrum in Ithyceridae appears somewhat similar to Nemonychidae in the position of the occipital sulci and mandibular tendons, though it lacks distinct subgenal sulci and the associated apodemes. Near the apex, the similarity tends more towards Brentidae, particularly in the weakly-developed apodemes of the hypostomal-labial sulci. The pleurostomal sulci are distinct.

Brentidae (Figs. 19-21):

*Brentinae* (Fig. 19): The rostal structure of this group appears quite similar to Caridae along the middle portion of the rostrum, though substantially differs near the base (adjacent to the antennal insertion) and at the apex. Nearer to the rostral base, the mandibular adductor tendons assume a slight dorsal position above the abductors. Also, while the tendons of the antennae usually move rather freely within the rostrum, small cuticular canals are present dorso-laterally in Brentinae to receive these tendons. The pleurostomal sulci are distinct.

*Apioninae* (Fig. 20): This group is similar to Brentinae in which the occipital sulci and apodemes are ventral on the rostrum, though the apodemes are fused medially for nearly the entire length of the rostrum. Any modifications for reception of the antennal apodemes do not appear to be present. The pharyngeal plate is larger and more sclerotized, and the pleurostomal sulci are distinct.

*Nanophyinae* (Fig. 21): While Nanophyinae also maintains some similarity with Brentinae, the occipital sulci and apodemes are more distanced from each other and positioned at the ventro-lateral corners of the rostrum. These sulci also do not join medially. The apodemes of the hypostomal-labial sulci are similar to those of Brentinae in being quite thin and appearing rather frail, though are apparently fused to form one medial apodeme in this subfamily. The pleurostomal sulci are distinct.

<u>Brachyceridae (Fig. 22)</u>:

The occipital sulci and apodemes are positioned more laterally and are somewhat elevated from the ventral floor of the rostrum in the brachycerids. Somewhat similar to

Apioninae, the apodemes of the occipital sulci also merge medially. The pleurostomal sulci are distinct.

Raymondionymidae (Fig. 23):

The occipital sulci in this group are positioned similarly to those in Brachyceridae, although the apodemes are fairly short and do not meet medially. The apodemes of the hypostomal-labial sulci are weakly-developed near the rostral apex, but become thicker and more robust slightly posteriorly before disappearing. The pleurostomal sulci are distinct.

Erirhinidae (Fig. 24):

This family is similar to Raymondionymidae, possessing more laterally positioned occipital sulci with separated apodemes. The pleurostomal sulci are distinct.

Dryophthoridae (Figs. 25-26):

Beginning in this family and continuing throughout the Curculionidae, the number and position of sulci remains moderately stable and the pleurostomal sulci are lost. The pharyngeal plate and apodemes of the hypostomal-labial sulci are well-developed and sclerotized with exocuticle. As the occipital sulci are positioned more ventro-laterally, the mandibular abductor tendons are held slightly dorsal to the adductors and maxillary tendons.

Curculionidae (Figs. 27-40):

Although the subgenal sulci and apodemes are absent in this family, it perhaps possesses the most diversity in terms of internal rostral structure. The occipital sulci seem to be similarly positioned ventrally in all curculionid lineages; however, the form of their apodemes varies rather dramatically between subfamilies and remains fairly stable within subfamilies.

*Bagoinae* (Fig. 27): While classified in Curculionidae, this group is perhaps the most aberrant in possessing distinct pleurostomal sulci. The cuticle is comparatively thin, similar to that in Mesoptilinae, Conoderinae, and many Entiminae. The apodemes of the occipital sulci are fairly raised above the ventral floor of the rostrum and they merge medially.

*Molytinae* (Fig. 28): Molytinae bears a fairly typical sulci and tendon orientation, the occipital sulci adjacent to the lateral corners of the rostrum and the apodemes short, separated, and resting on the ventral floor of the rostrum. The mandibular adductor tendons are located mesial and slightly dorsal to the abductor tendons.

*Lixinae* (Fig. 29): This group is fairly similar to Molytinae, although the apodemes of the occipital sulci hold the tendons slightly more elevated from the ventral floor of the rostrum. Towards to rostral base, the apodemes nearly merge medially due to the constriction of the antennal scrobe.

*Hyperinae* (Fig. 30): Hyperinae is quite similar to Lixinae, differing mostly in not possessing a strong basal constriction of the rostrum, causing the apodemes of the occipital sulci to approximate one another.

*Baridinae* (Fig. 31): Baridinae and a few other subfamilies have evolved more derived and elaborate apodemal complexes for holding the tendons. Again, the occipital sulci are positioned ventrally, while the apodemes have formed a tiered structure caused by the medio-ventral migration of the mandibular abductor tendons and their associated apodeme under the adductor tendons and their apodeme. The resulting structure is akin to a ventral tunnel, through which the mandibular abductor tendons pass, and a dorsal shelf supporting the mandibular adductors on the sides and the maxillary tendons in the middle.

*Cyclominae* (Fig. 32): As the occipital sulci are positioned more ventro-laterally in this group, the apodemes do not merge medially. The mandibular adductor tendons are held dorsally, while the abductor tendons are immediately ventral, enclosed in a tunnel formed by the apodemes.

*Cryptorhynchinae* (Fig. 33): This subfamily appears nearly identical to Cyclominae, in which the apodemes and tendons are vertically stratified at the lateral corners of the rostrum. Near the rostral apex, however, the apodemes of the hypostomal-labial sulci fuse medially, forming an X-shaped scaffold.

*Cossoninae* (Fig. 34): Cossoninae is fairly similar to Cyclominae and Cryptorhynchinae with stratified apodemes. It is perhaps most alike to Baridinae, however, by the more proximal occipital sulci which allow for the medial fusion of the apodemes. The apodemes of the hypostomal-labial sulci also fuse medially.

*Conoderinae* (Fig. 35): The structure of the apodemes and position of occipital sulci along much of the rostrum in Conoderinae is nearly identical to Bagoinae. The major difference lies in a slight alteration in the arrangement of maxillary tendons. Also, as in the former few subfamilies, the apodemes of the hypostomal-labial sulci fuse medially.

*Mesoptilinae* (Fig. 36): This family displays another distinct vertical stratification of the apodemes of the occipital sulci, similar to that present in Cossoninae. The medial fusion of the apodemes of the hypostomal-labial sulci is also present, though the apodemes are somewhat less robust. The mandibular adductor tendons are also rather enlarged and oblong.

*Ceutorhynchinae* (Fig. 37): The internal rostrum structure in this group is remarkably similar along the entire length to that in Molytinae and Hyperinae. The occipital sulci are positioned more ventro-medially, in which the mandibular adductor tendons are situated mesial to the abductors, and the apodemes of the hypostomal-labial sulci are separate.

*Entiminae* (Fig. 38): Although members of Entiminae often possess a shortened rostrum, its structure is akin to that of Conoderinae and Bagoinae. The apodemes of the occipital sulci are slightly elevated from the ventral floor of the rostrum and, in taxa bearing a longer rostrum, the mandibular adductor tendons also rest on these apodemes. A major difference is that the apodemes of the hypostomal-labial sulci are separate and less robust.

*Curculioninae* (Figs. 39-40): This group is most similar to Ceutorhynchinae and Lixinae. While the apodemes of the hypostomal-labial sulci fuse medially, they are less robust and very slender.

**Discussion**

Aside from differences in the basal gular region of the head, the most notable changes in rostrum evolution within Curculionoidea appear to lie in orientation of the ventral sulci (occipital and subgenal) and location and degree of development of the internal apodemes/phragma that usually are denoted by these sulci (Fig. 3). Apically, most Curculionoidea (excluding Scolytidae and Platypodidae) possess an internal, X-shaped scaffold extending from the postmentum and hypostomal-labial sulci which support the mandibular adductor tendons and the beginning of the pharynx. In the lower weevils (all families except Curculionidae), the occipital sulcus is positioned more laterally on the rostrum, which is apparent from the lateral phragma that support the mandibular adductor and abductor tendons. While the subgenal sulci appear to be visible externally in several of these basal families, they do not form any internalized presence. In the higher Curculionoidea (Curculionidae *s. lat.*), the occipital sulci have migrated ventrally and the subgenal sulci appear largely internalized and invisible externally, possibly either subsumed into the bridge between the apodemes of the occipital sulci or lost.

Due to the absence of a rostrum in Scolytidae and Platypodidae, any evidence of internal apodemes seems to have also disappeared. Examination of the internal, pre-ocular region of the head in these groups, therefore, although appearing little informative in elucidating their phylogenetic placements, requires further study in different taxa. Despite these problems, internal rostrum structure does seem to provide further support for Curculionidae *s. lat.* Of the taxa studied, Scolytidae + Platypodidae appear to form a monophyletic group more towards the base of Curculionoidea. Within Curculionidae, in which both the pleurostomal and subgenal sulci have been lost, there appears to be greater differentiation and plasticity of the apodemes of the occipital sulci than in the more basal families. Perhaps possessing both separate sets of ventral sulci imposes constraints on the degree to which they may be modified. Following further sampling, the structural differences seen in the internal rostral apodemes may become more informative of classificatory groupings within Curculionidae.

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I owe much gratitude to my advisor, Dr. M.S. Engel, who has guided and supported me through every step of this project. Much appreciation is given to the assistance and support of the staff at the University of Kansas Microscopy and Analytical Imaging Laboratory throughout much of this project and particularly during thin sectioning, staining, and imaging, including Dr. David Moore, Dr. Bruce Cutler (retired), and Heather Shinogle. Partial funding for microscopy was provided by NSF DEB-1110590 (to M.S. Engel, P. Cartwright, and S.R. Davis).

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## Figure legends

**Fig. 1**. Strict consensus tree of 1476 most-parsimonious trees, L= 112, Ci=19, Ri=35 (MP trees of L=55, Ci=40, Ri=76). 1a, characters mapped on via fast optimization (ACCTRAN); 1b, characters mapped on via slow optimization (DELTRAN).

**Fig. 2**. 50% majority rules tree, L=65, Ci=33, Ri=69.

**Fig. 3**. General model of a section of the weevil rostrum, illustrating the relative position of key internal structures.

**Fig. 4**. Semi-thin sections of head of *Salpingus pallipes* (Salpingidae). A, ventral aspect of head; B, lateral aspect of head; C-F, sections; G, legend for illustrations of sections.

**Fig. 5**. Semi-thin sections of head of *Diabrotica undecimpunctata* (Chrysomelidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 6**. Semi-thin sections of head of Nemonychidae. A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 7**. Semi-thin sections of head of Anthribidae. A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 8**. Semi-thin sections of head of Anthribidae. A, ventral aspect of head; B, lateral aspect of head; C-J, sections.

**Fig. 9**. Semi-thin sections of head of Belidae. A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 10**. Semi-thin sections of head of Attelabinae (Attelabidae). A, ventral aspect of head; B, lateral aspect of head; C-E, SEM's of anterior region of oral cavity, showing remnant of anterior tentorial arms; F-J, sections.

**Fig. 11**. Semi-thin sections of head of Attelabinae (Attelabidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 12**. Semi-thin sections of head of Rhynchitinae (Attelabidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 13**. Semi-thin sections of head of Scolytinae (Scolytidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 14**. Semi-thin sections of head of Scolytinae (Scolytidae). A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 15**. Semi-thin sections of head of Hylesininae (Scolytidae). A, ventral aspect of head; B, lateral aspect of head; C-J, sections.

**Fig. 16**. Semi-thin sections of head of Platypodidae. A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 17**. Semi-thin sections of head of Caridae. A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 18**. Semi-thin sections of head of Ithyceridae. A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 19**. Semi-thin sections of head of Brentinae (Brentidae). A, ventral aspect of head; B, lateral aspect of head; C-J, sections.

**Fig. 20**. Semi-thin sections of head of Apioninae (Brentidae). A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 21**. Semi-thin sections of head of Nanophyinae (Brentidae). A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 22**. Semi-thin sections of head of Brachyceridae. A, ventral aspect of head; B, lateral aspect of head; C-E, sections.

**Fig. 23**. Semi-thin sections of head of Raymondionymidae. A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 24**. Semi-thin sections of head of Erirhinidae. A, ventral aspect of head; B, lateral aspect of head; C-J, sections.

**Fig. 25**. Semi-thin sections of head of Dryophthoridae. A, ventral aspect of head; B, lateral aspect of head; C-F, sections.

**Fig. 26**. Semi-thin sections of head of Dryophthoridae. A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 27**. Semi-thin sections of head of Bagoinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 28**. Semi-thin sections of head of Molytinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 29**. Semi-thin sections of head of Lixinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 30**. Semi-thin sections of head of Hyperinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 31**. Semi-thin sections of head of Baridinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 32**. Semi-thin sections of head of Cyclominae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 33**. Semi-thin sections of head of Cryptorhynchinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 34**. Semi-thin sections of head of Cossoninae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-I, sections.

**Fig. 35**. Semi-thin sections of head of Conoderinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

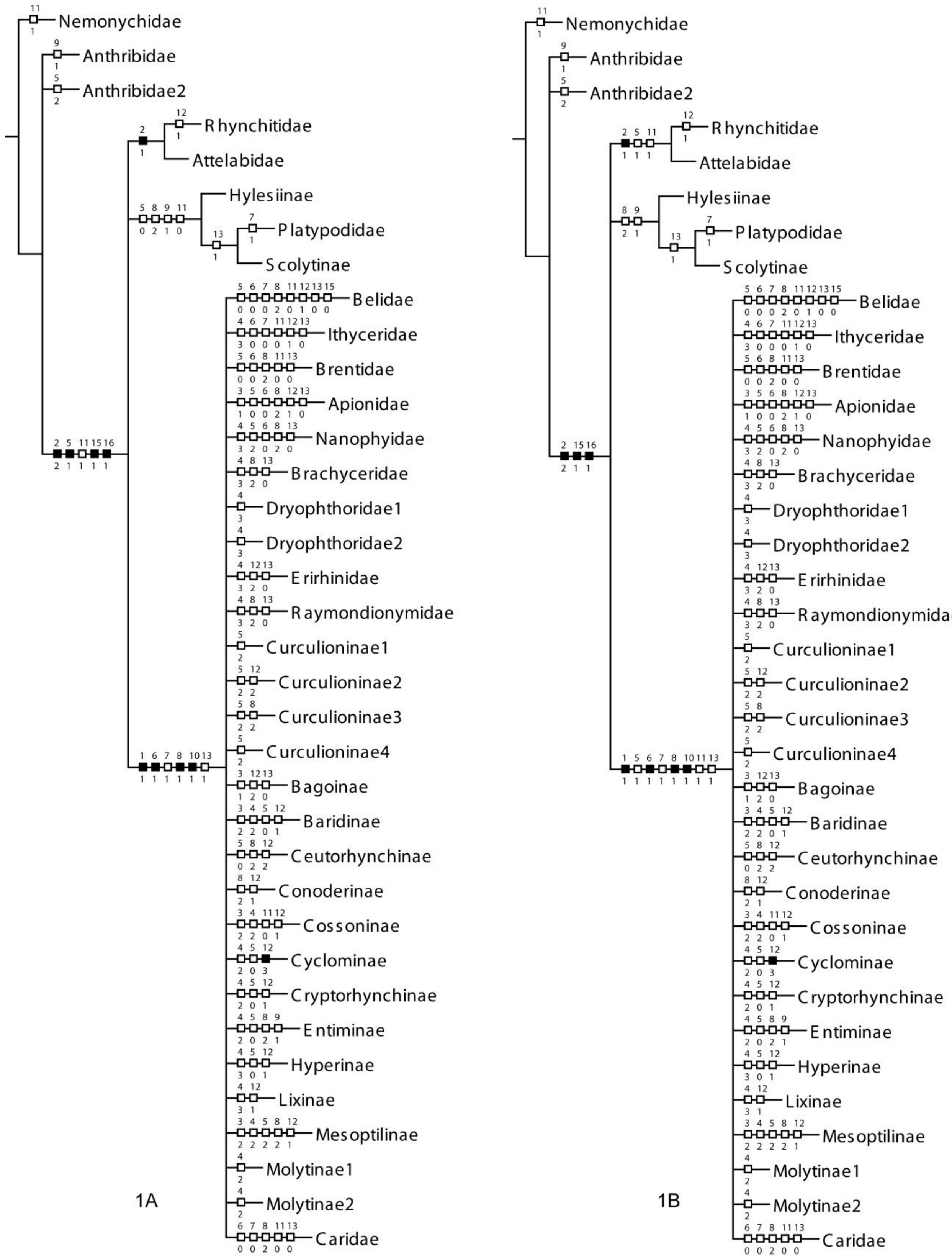
**Fig. 36**. Semi-thin sections of head of Mesoptilinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 37**. Semi-thin sections of head of Ceutorhychinae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.

**Fig. 38**. Semi-thin sections of head of Entiminae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-G, sections.

**Fig. 39**. Semi-thin sections of head of *Curculio* sp. (Curculionidae: Curculioninae). A, lateral aspect of head; B-G, sections.

**Fig. 40**. Semi-thin sections of head of Curculioninae (Curculionidae). A, ventral aspect of head; B, lateral aspect of head; C-H, sections.


Nemonychidae
Anthribidae
Anthribidae2
Rhynchitidae
Attelabidae
Hylesiinae
Platypodidae
Scolytinae
Belidae
Ithyceridae
Brentidae
Apionidae
Nanophyidae
Brachyceridae
Dryophthoridae1
Dryophthoridae2
Erirhinidae
Raymondionymidae
Curculioninae1
Curculioninae2
Curculioninae3
Curculioninae4
Bagoinae
Baridinae
Ceutorhynchinae
Conoderinae
Cossoninae
Cyclominae
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Hyperinae
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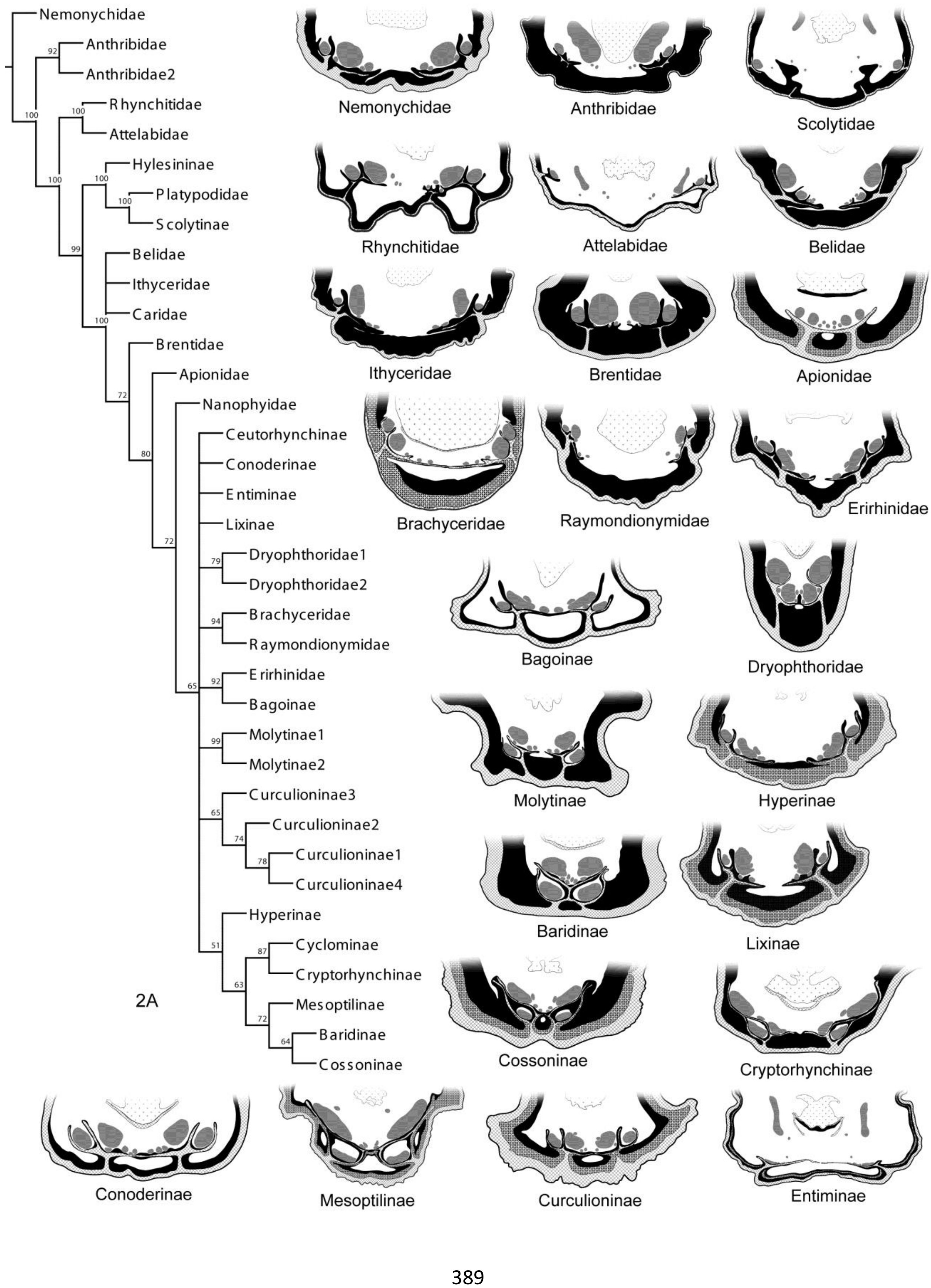
Mesoptilinae
Molytinae1
Molytinae2
Caridae

1A

1B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99
Belidae
Ithyceridae
Caridae
100
Brentidae
72
Apionidae
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Nanophyidae
Ceutorhynchinae
Conoderinae
Entiminae
Lixinae
72
79
Dryophthoridae1
Dryophthoridae2
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Brachyceridae
Raymondionymidae
65
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Erirhinidae
Bagoinae
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Molytinae1
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Curculioninae3
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Curculioninae2
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Curculioninae1
Curculioninae4
Hyperinae
51
87
Cyclominae
Cryptorhynchinae
63
Mesoptilinae
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64
Baridinae
Cossoninae
2A
Nemonychidae
Anthribidae
Scolytidae
Rhynchitidae
Attelabidae
Belidae
Ithyceridae
Brentidae
Apionidae
Brachyceridae
Raymondionymidae
Erirhinidae
Bagoinae
Dryophthoridae
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Lixinae
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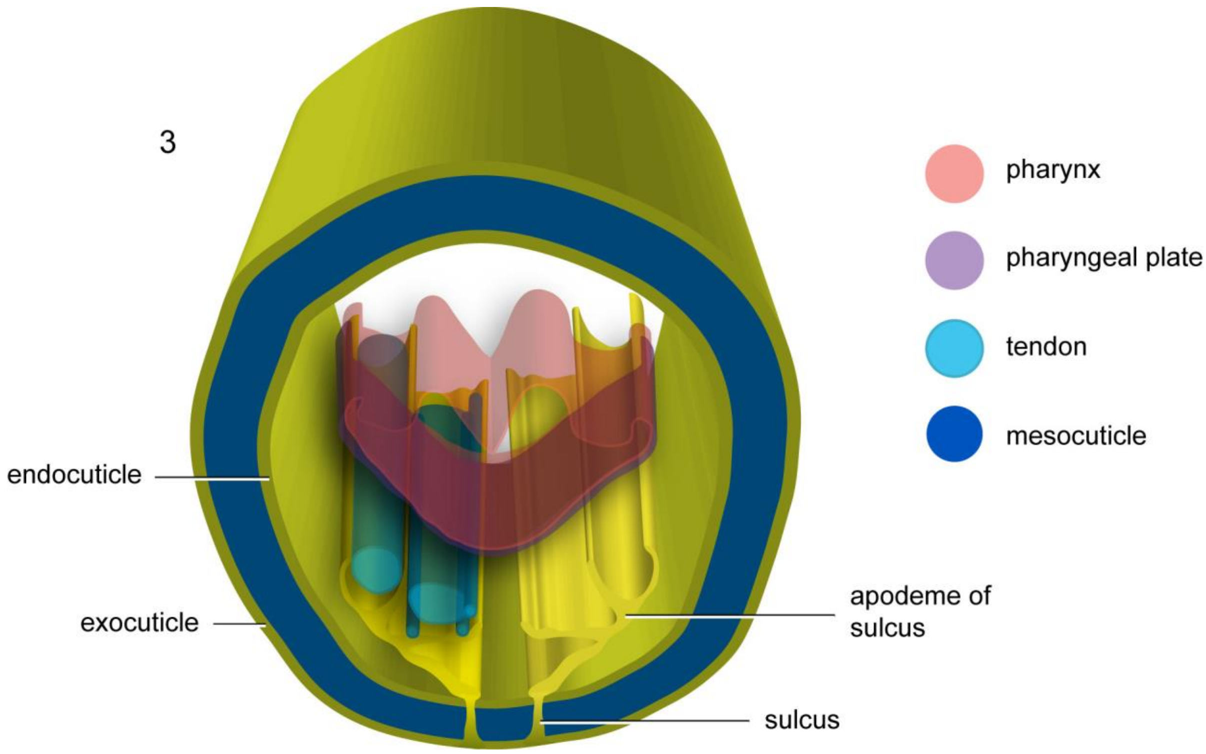
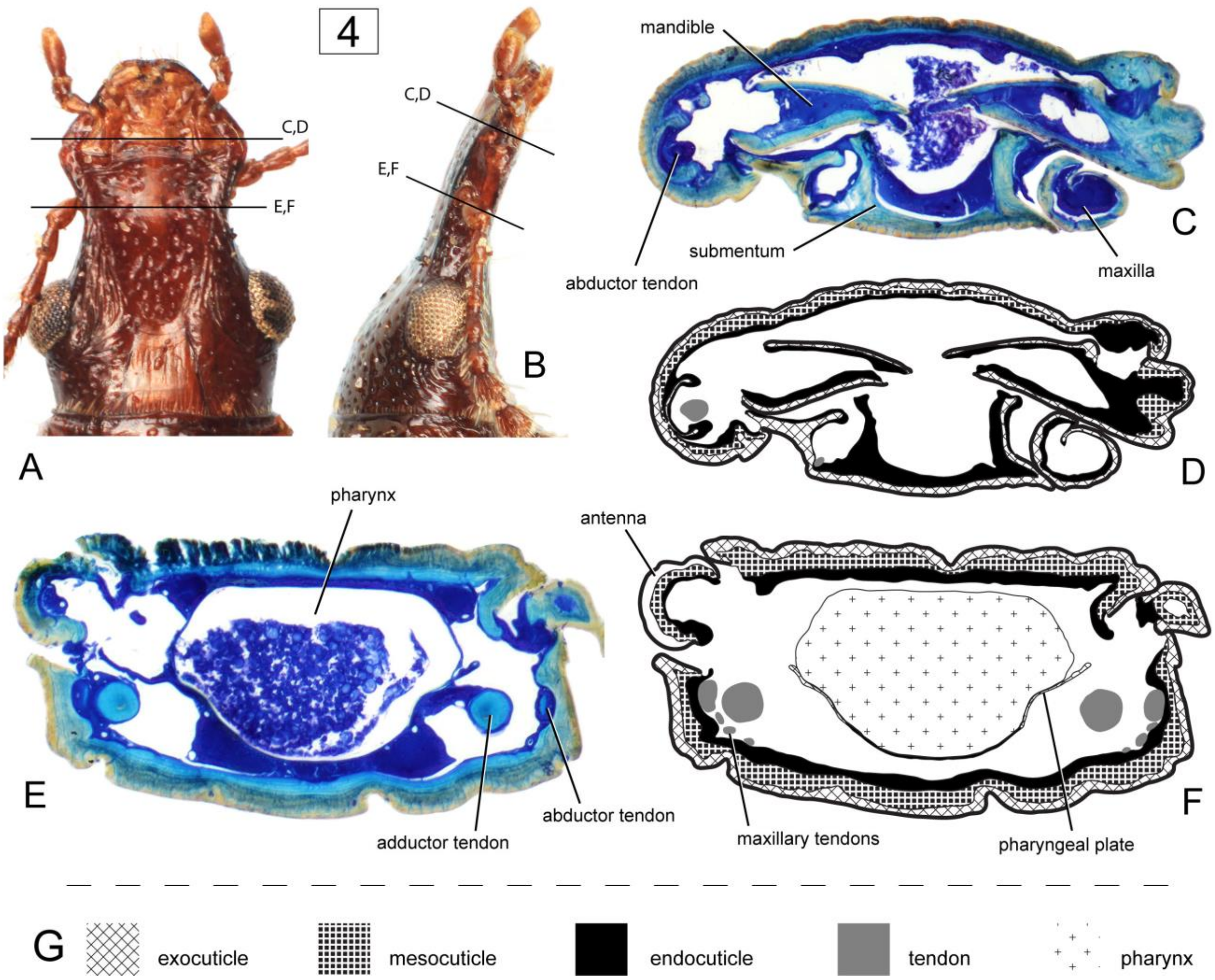
Cryptorhynchinae
Conoderinae
Mesoptilinae
Curculioninae
Entiminae

3


pharynx
pharyngeal plate
tendon
mesocuticle
endocuticle
exocuticle
apodeme of sulcus
sulcus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C,D
E,F
A
B
mandible
abductor tendon
submentum
maxilla
C
D
pharynx
antenna
E
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abductor tendon
maxillary tendons
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F
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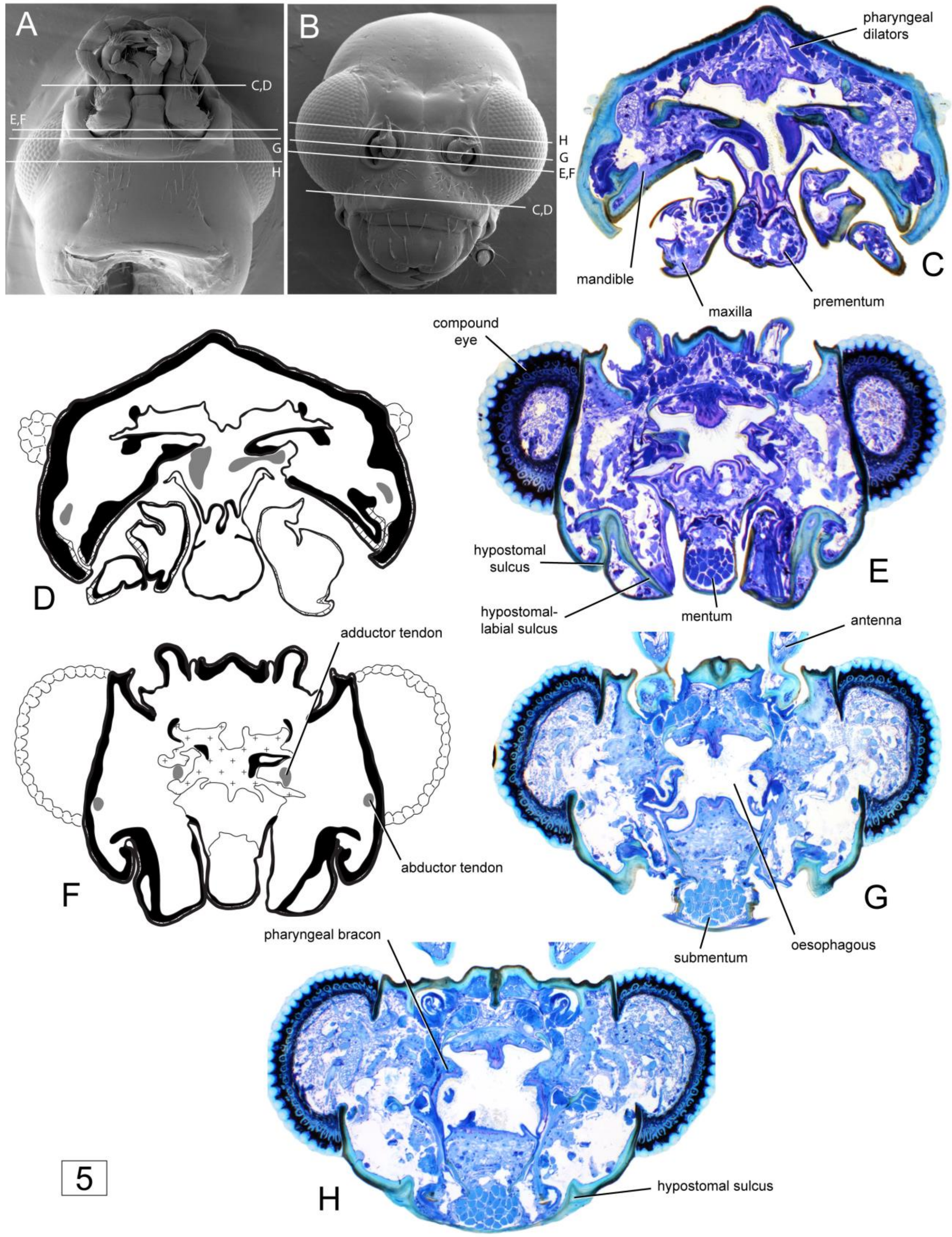
exocuticle
mesocuticle
endocuticle
tendon
pharynx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C,D
E,F
G
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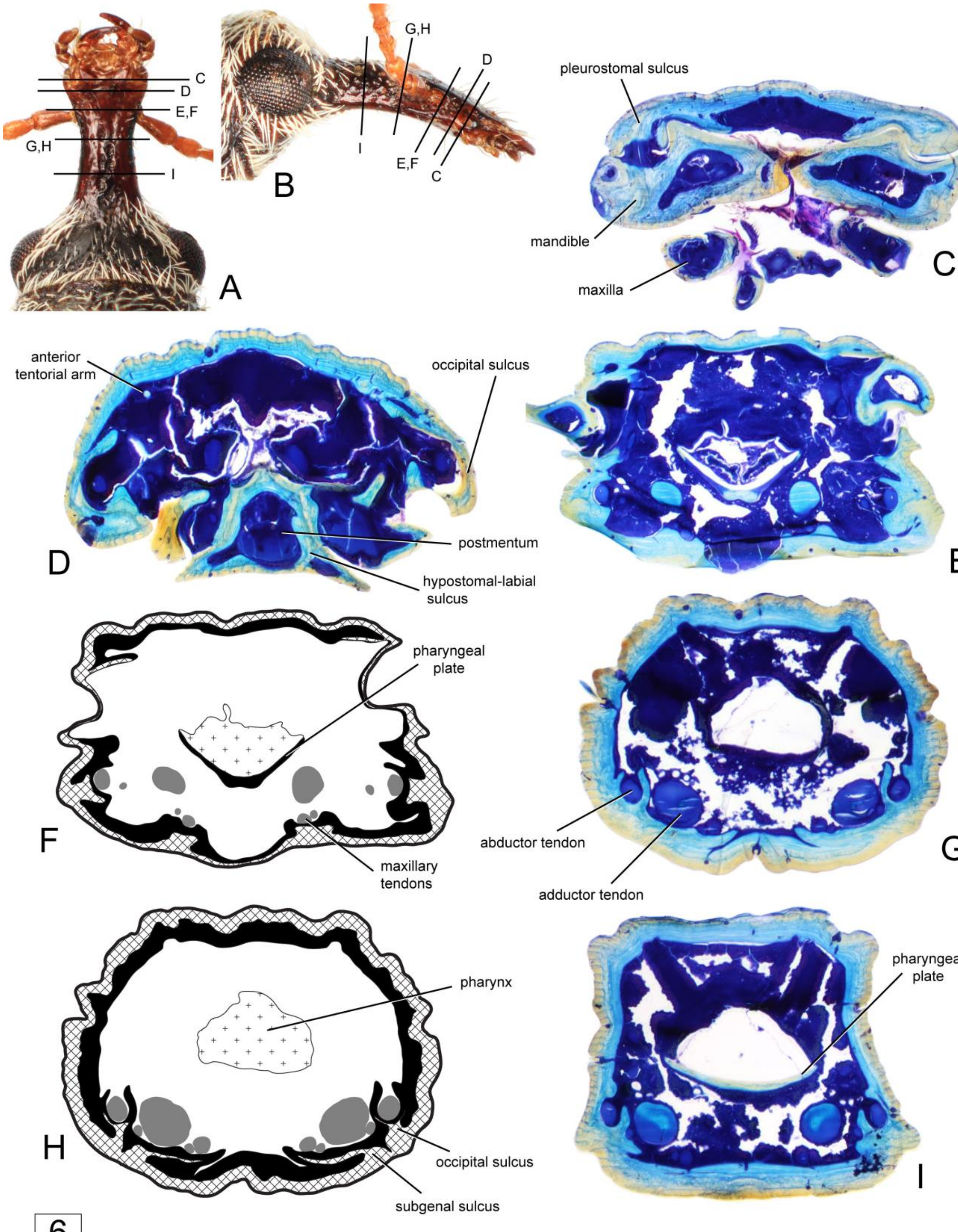
G
E,F
C,D
pharyngeal
dilators
mandible
maxilla
prementum
C
compound
eye
hypostomal
sulcus
hypostomal-
labial sulcus
mentum
E
D
adductor tendon
abductor tendon
F
antenna
G
submentum
oesophagous
pharyngeal bracon
hypostomal sulcus
H
5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E,F
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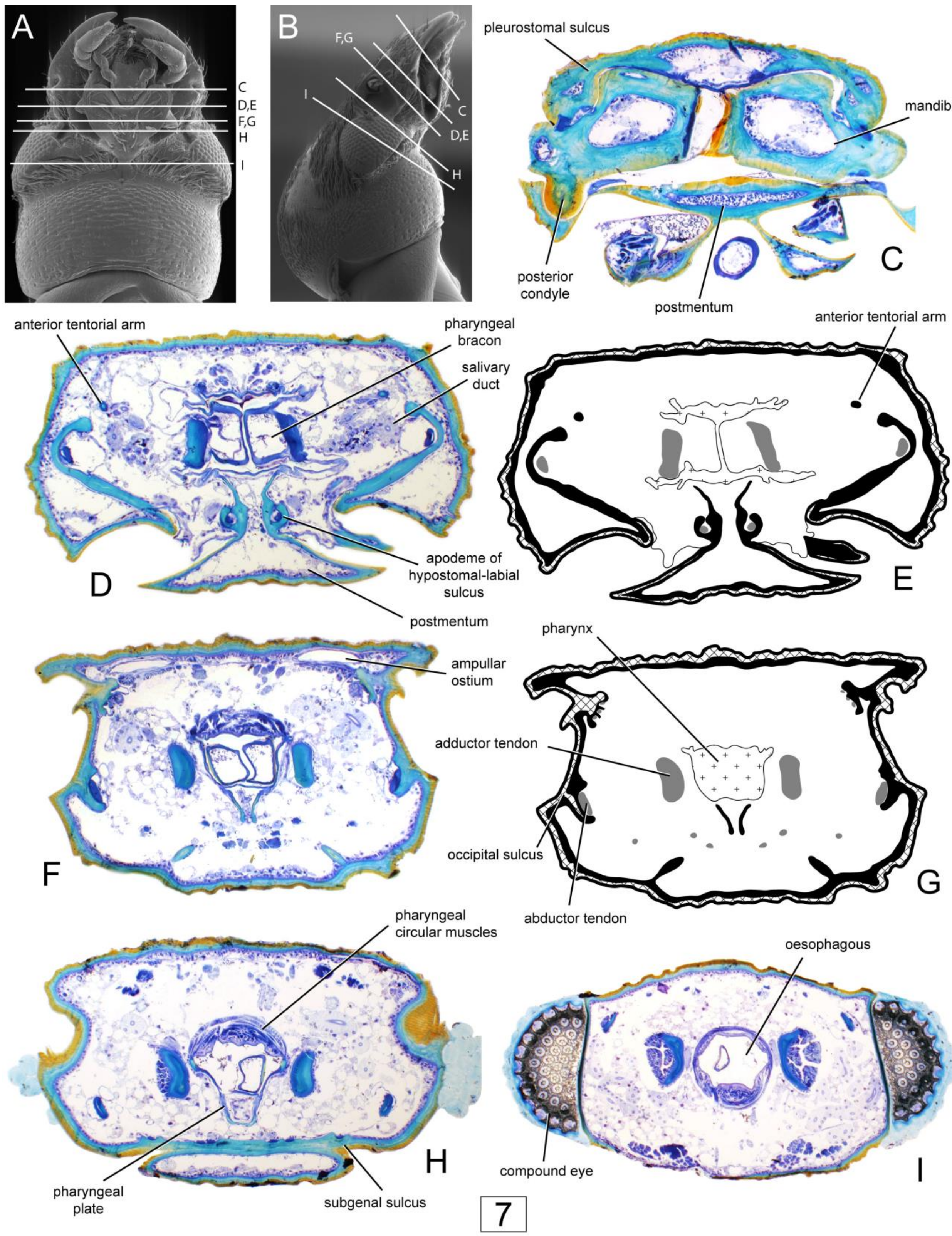
I
A
G,H
D
I
E,F
C
B
pleurostomal sulcus
mandible
maxilla
C
anterior
tentorial arm
occipital sulcus
postmentum
hypostomal-labial
sulcus
D
E
pharyngeal
plate
F
maxillary
tendons
abductor tendon
adductor tendon
G
pharynx
H
occipital sulcus
subgenal sulcus
pharyngeal
plate
I
6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B
C
D,E
F,G
H
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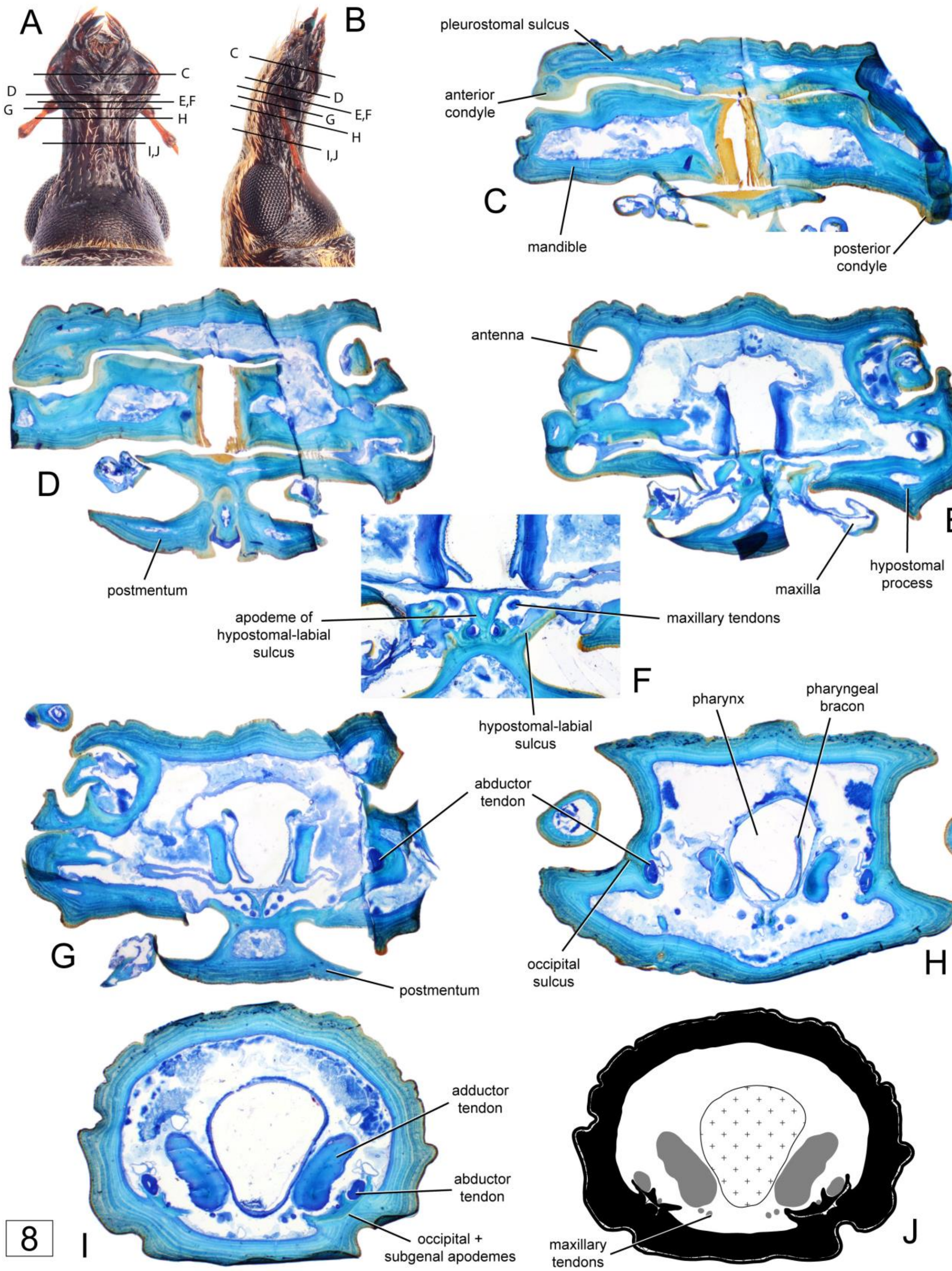
mandible
posterior condyle
postmentum
anterior tentorial arm
pharyngeal bracon
salivary duct
apodeme of hypostomal-labial sulcus
D
E
ampullar ostium
pharynx
adductor tendon
occipital sulcus
abductor tendon
F
G
pharyngeal circular muscles
oesophagous
pharyngeal plate
subgenal sulcus
compound eye
H
I
7


A
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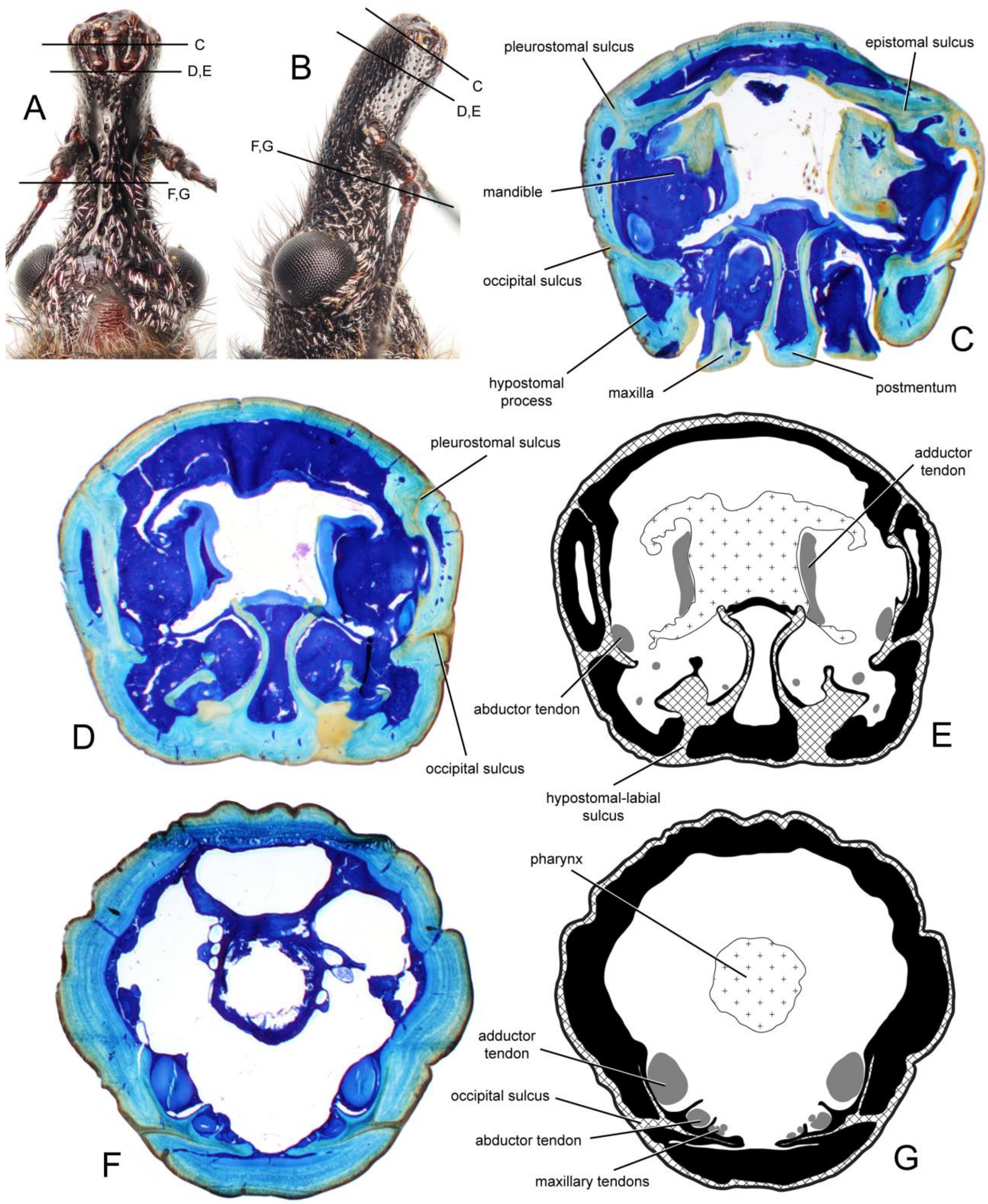
C
D
E,F
G
H
I,J
pleurostomal sulcus
anterior condyle
mandible
posterior condyle
antenna
postmentum
maxilla
hypostomal process
apodeme of hypostomal-labial sulcus
maxillary tendons
F
hypostomal-labial sulcus
pharynx
pharyngeal bracon
abductor tendon
occipital sulcus
postmentum
adductor tendon
abductor tendon
occipital + subgenal apodemes
maxillary tendons
8
I
J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C
D,E
F,G
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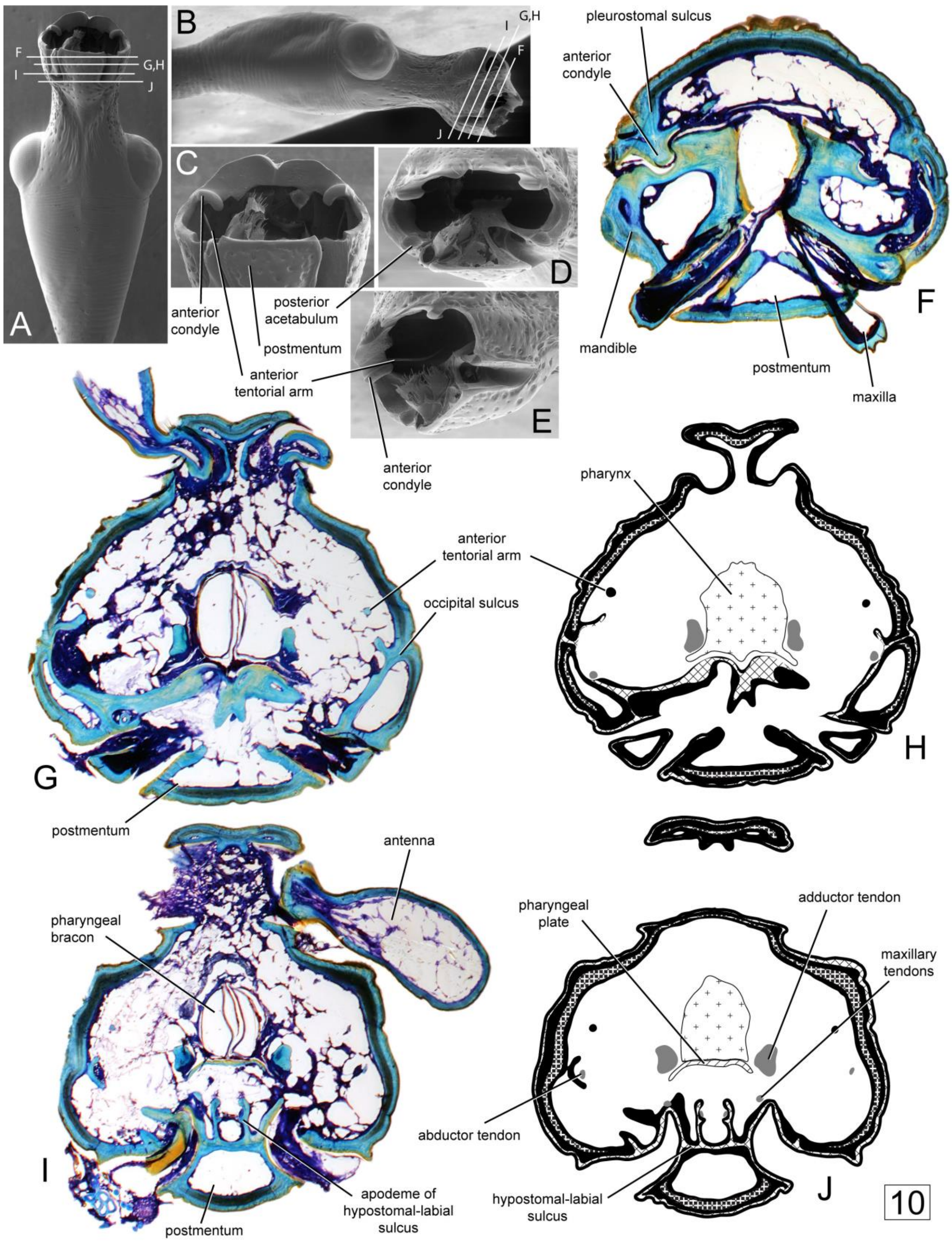
epistomal sulcus
mandible
occipital sulcus
hypostomal process
maxilla
postmentum
adductor tendon
abductor tendon
hypostomal-labial sulcus
pharynx
maxillary tendons
D
E
F
G

9


A
B
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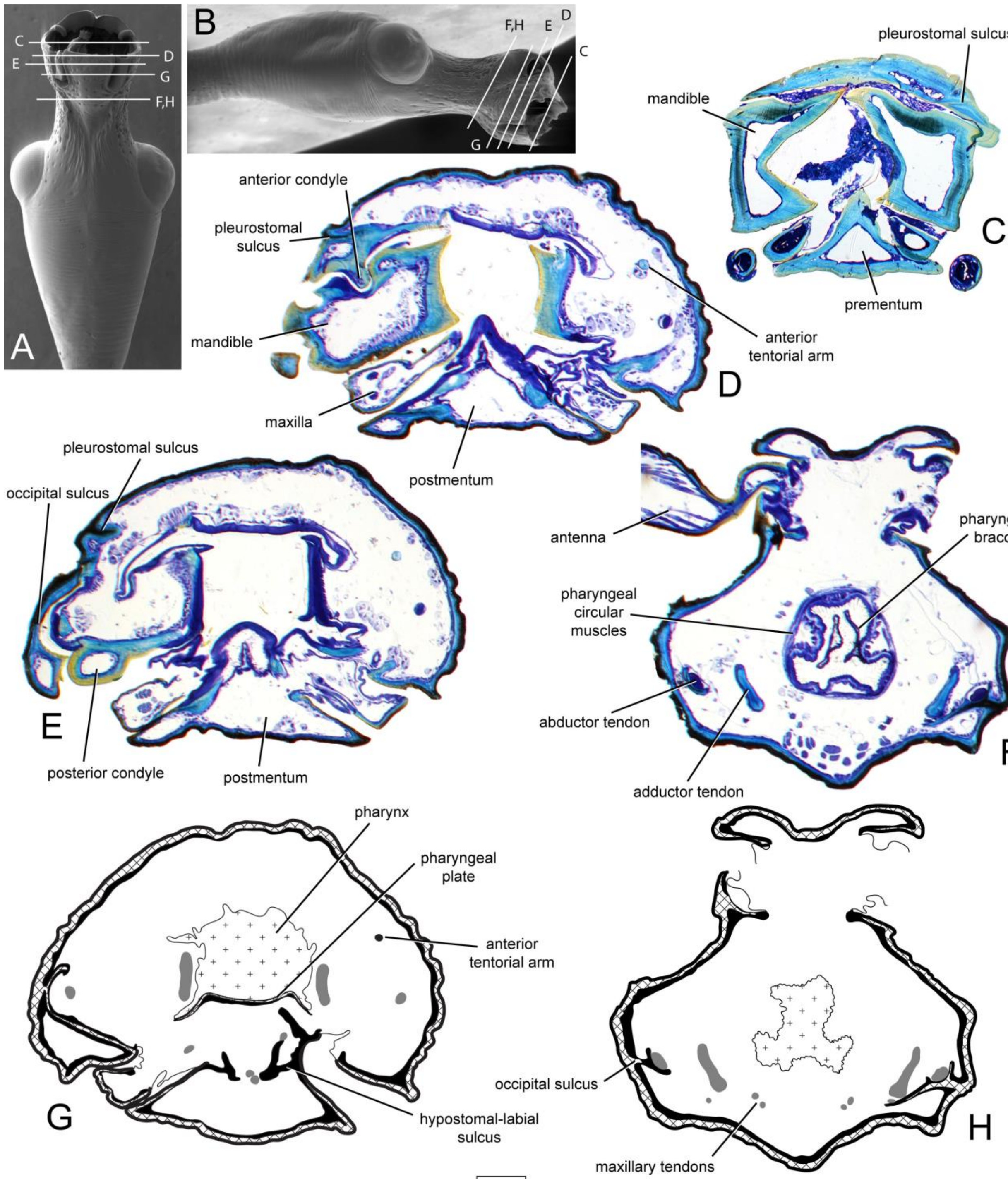
J
F
G,H
I
J
anterior condyle
postmentum
posterior acetabulum
anterior tentorial arm
anterior condyle
pleurostomal sulcus
anterior condyle
mandible
postmentum
maxilla
pharynx
anterior tentorial arm
occipital sulcus
postmentum
antenna
pharyngeal bracon
apodeme of hypostomal-labial sulcus
postmentum
pharyngeal plate
adductor tendon
maxillary tendons
abductor tendon
hypostomal-labial sulcus
10


C
D
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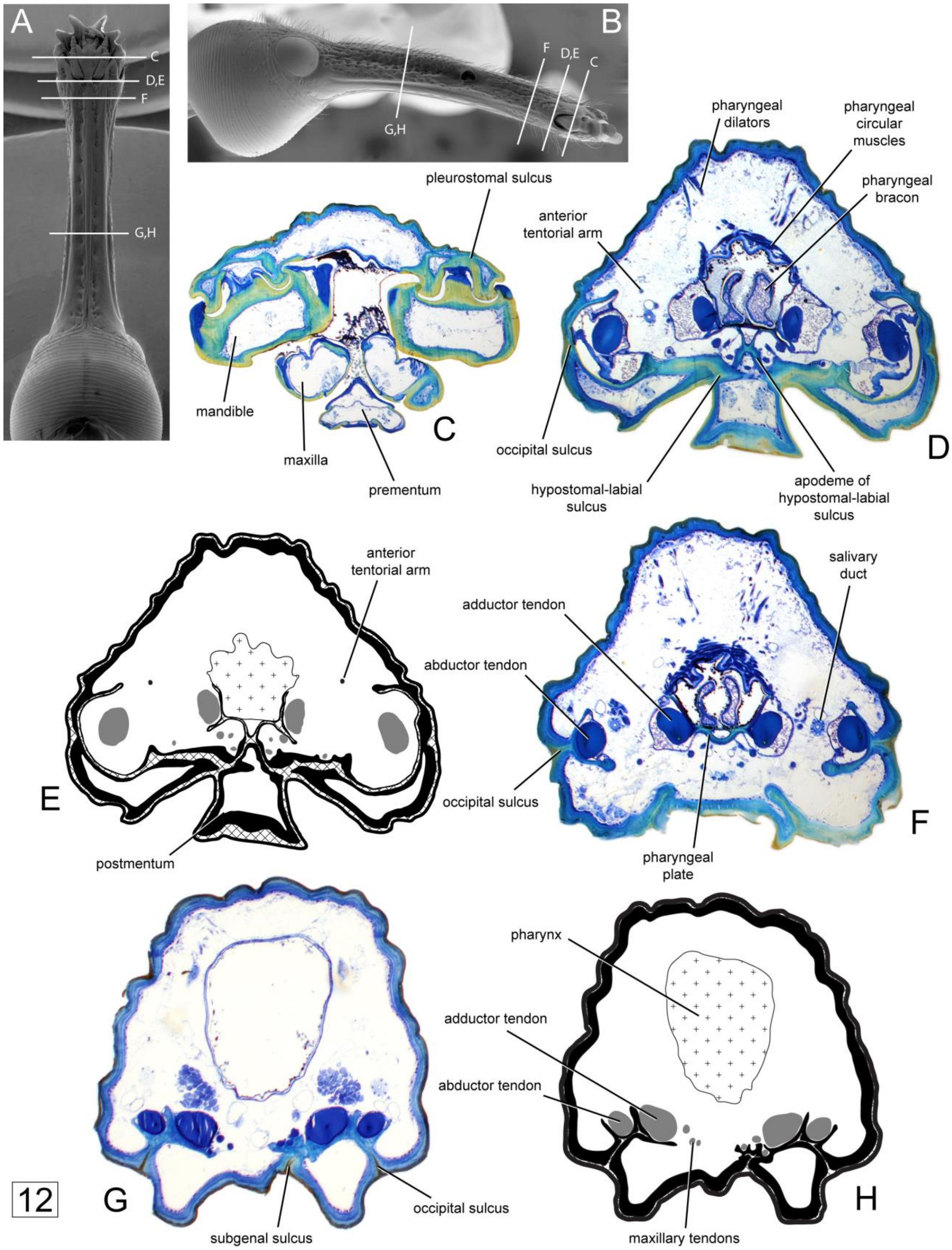
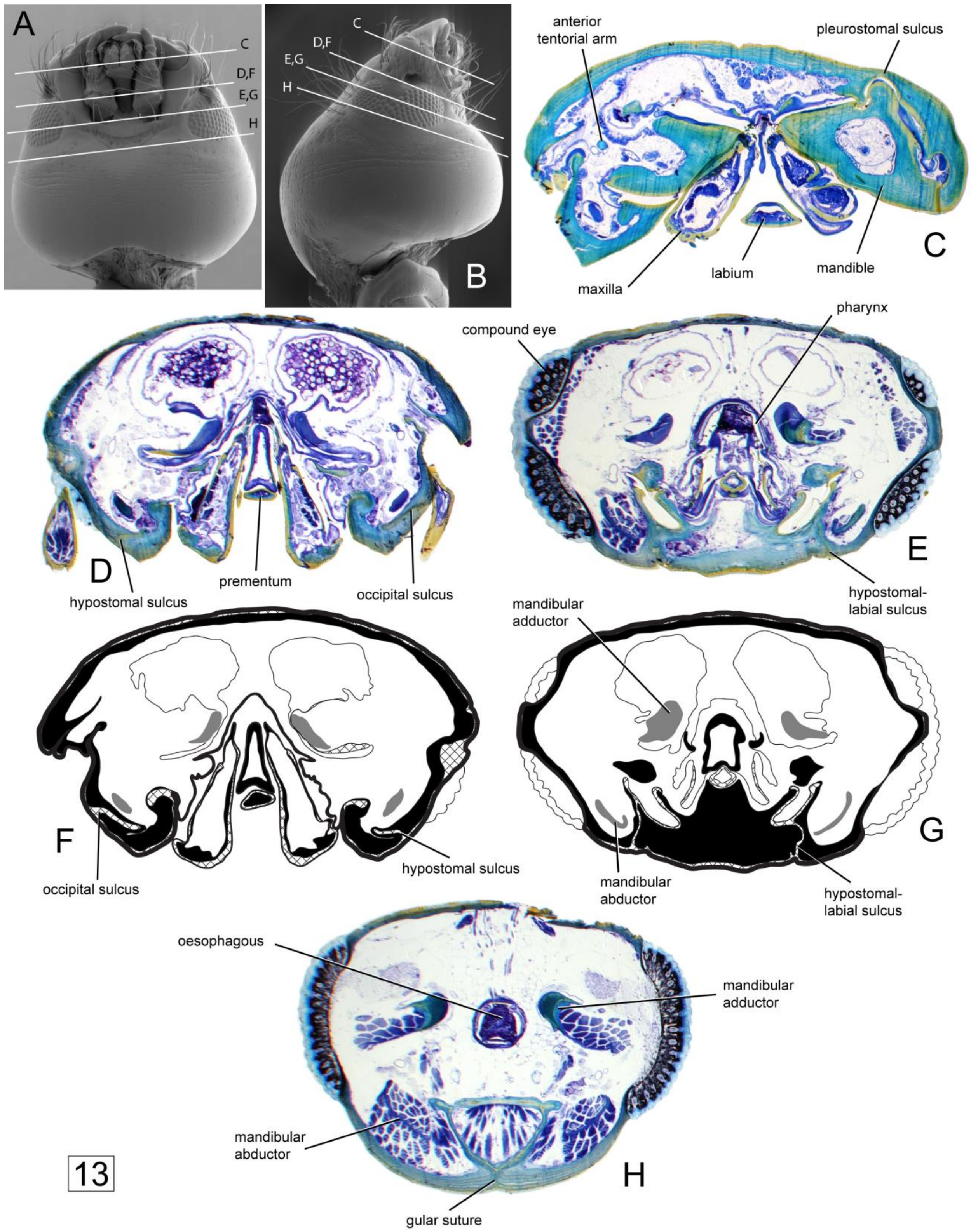
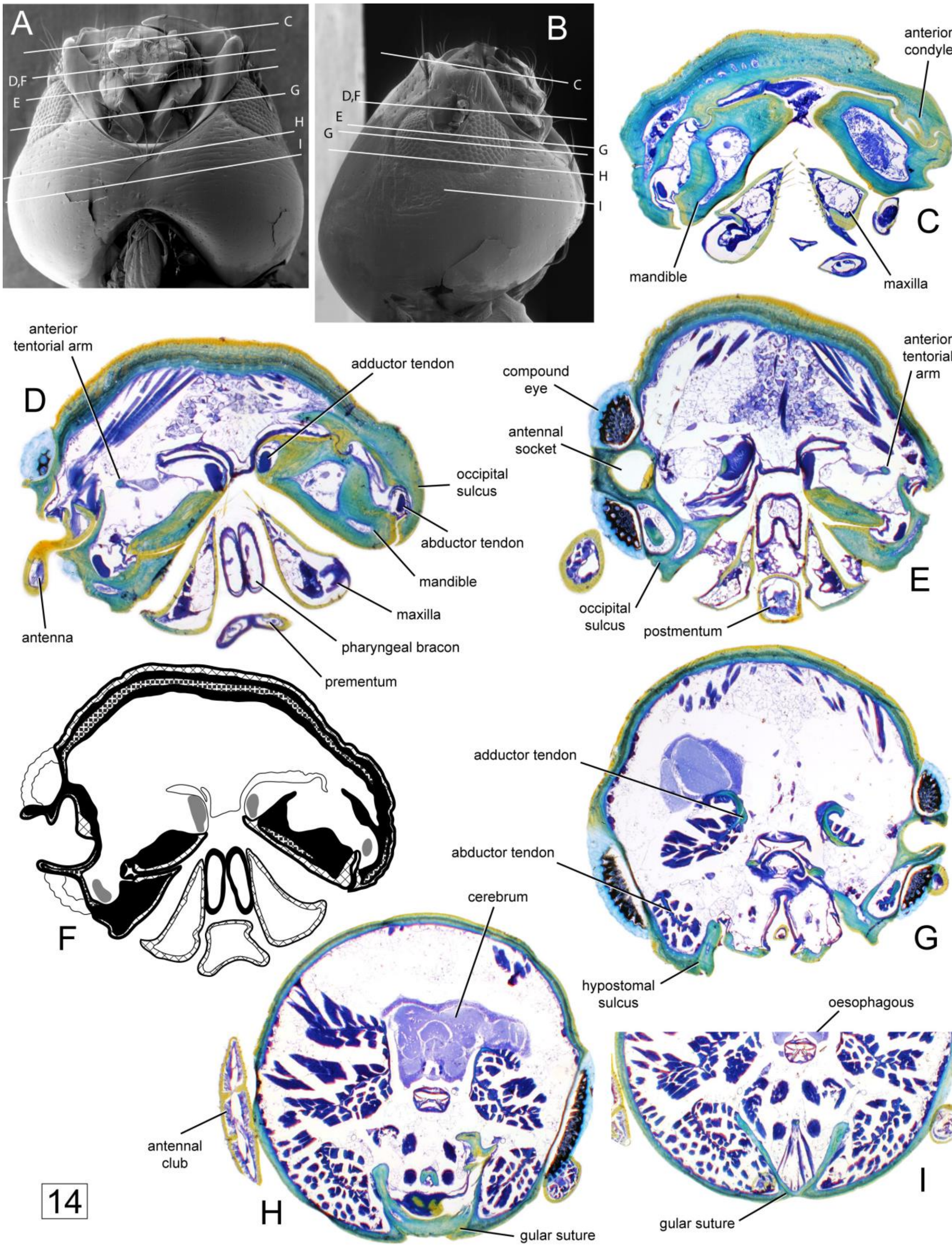
F,H
A
B
F,H
E
D
C
G
pleurostomal sulcus
mandible
C
prementum
anterior condyle
pleurostomal sulcus
mandible
maxilla
postmentum
anterior tentorial arm
D
pleurostomal sulcus
occipital sulcus
E
posterior condyle
postmentum
antenna
pharyngeal bracon
pharyngeal circular muscles
abductor tendon
adductor tendon
F
pharynx
pharyngeal plate
anterior tentorial arm
hypostomal-labial sulcus
G
occipital sulcus
maxillary tendons
H

11



A
C
D,E
F
G,H
B
F
D,E
C
G,H
pleurostomal sulcus
mandible
maxilla
prementum
C
pharyngeal dilators
pharyngeal circular muscles
pharyngeal bracon
anterior tentorial arm
occipital sulcus
hypostomal-labial sulcus
apodeme of hypostomal-labial sulcus
D
anterior tentorial arm
postmentum
E
salivary duct
adductor tendon
abductor tendon
occipital sulcus
pharyngeal plate
F
12
G
subgenal sulcus
occipital sulcus
pharynx
adductor tendon
abductor tendon
maxillary tendons
H


A
C
D,F
E,G
H
B
anterior tentorial arm
pleurostomal sulcus
maxilla
labium
mandible
compound eye
pharynx
D
hypostomal sulcus
prementum
occipital sulcus
E
hypostomal-labial sulcus
mandibular adductor
F
occipital sulcus
hypostomal sulcus
G
mandibular abductor
hypostomal-labial sulcus
oesophagous
mandibular adductor
mandibular abductor
H
gular suture
13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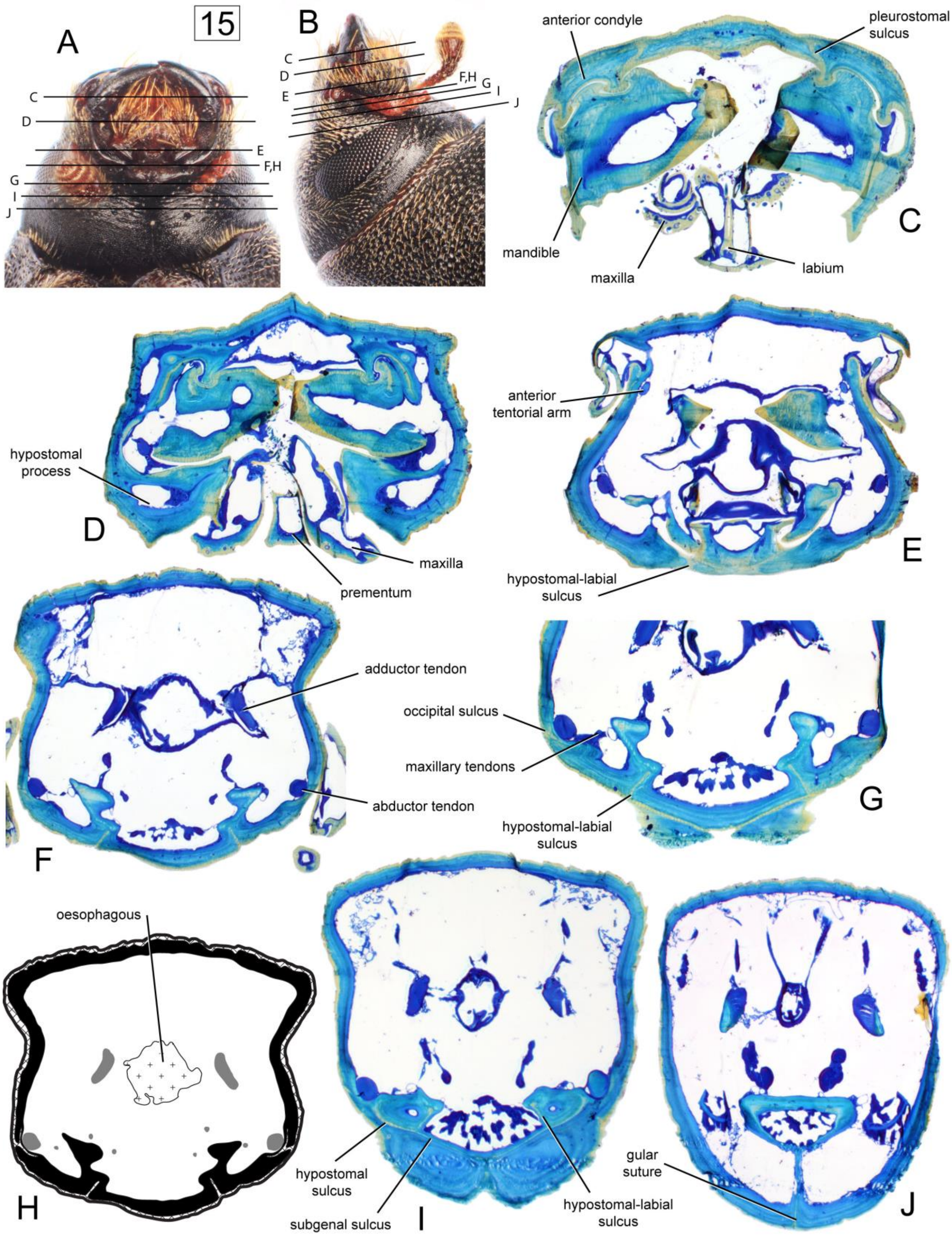
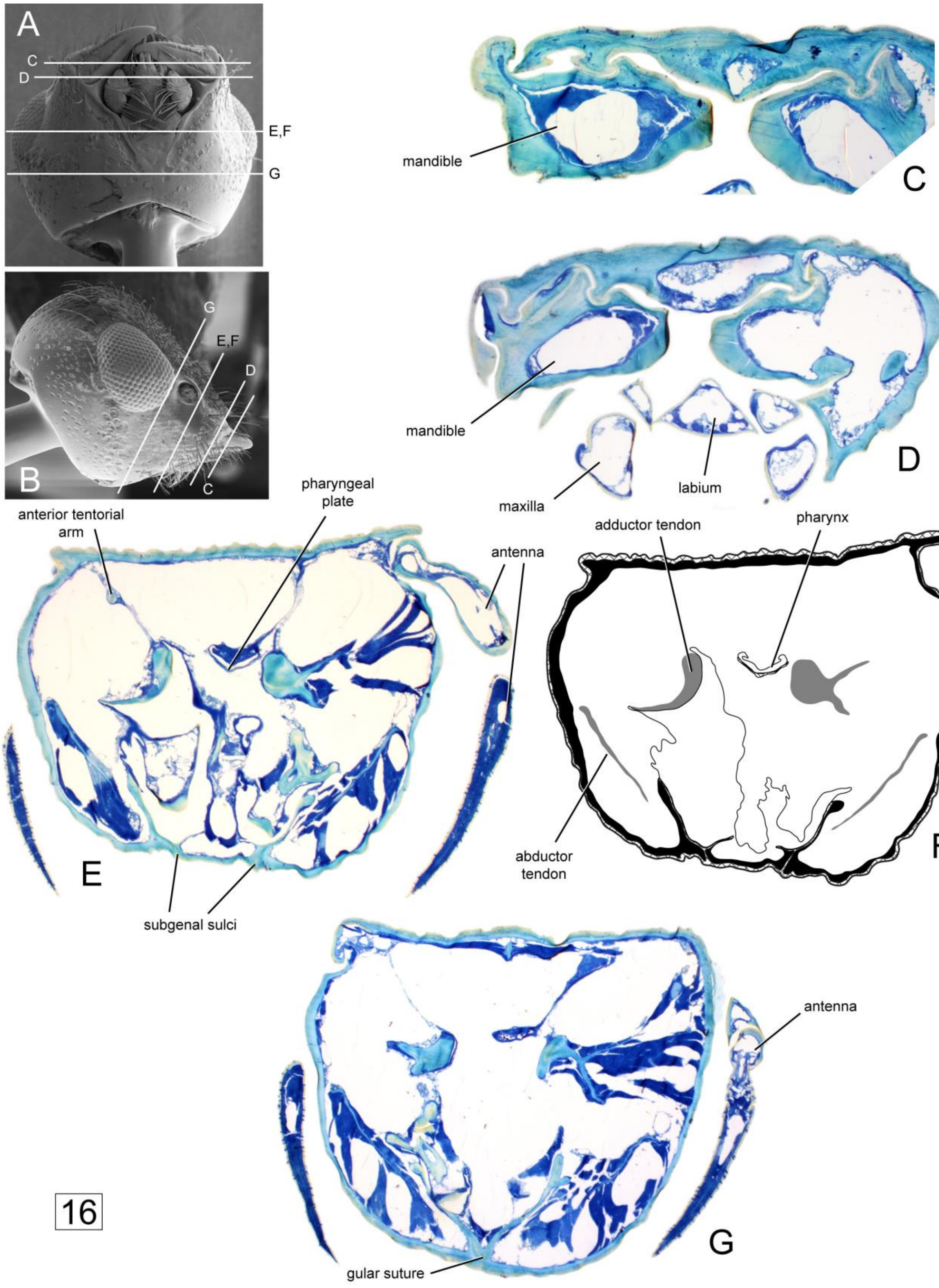
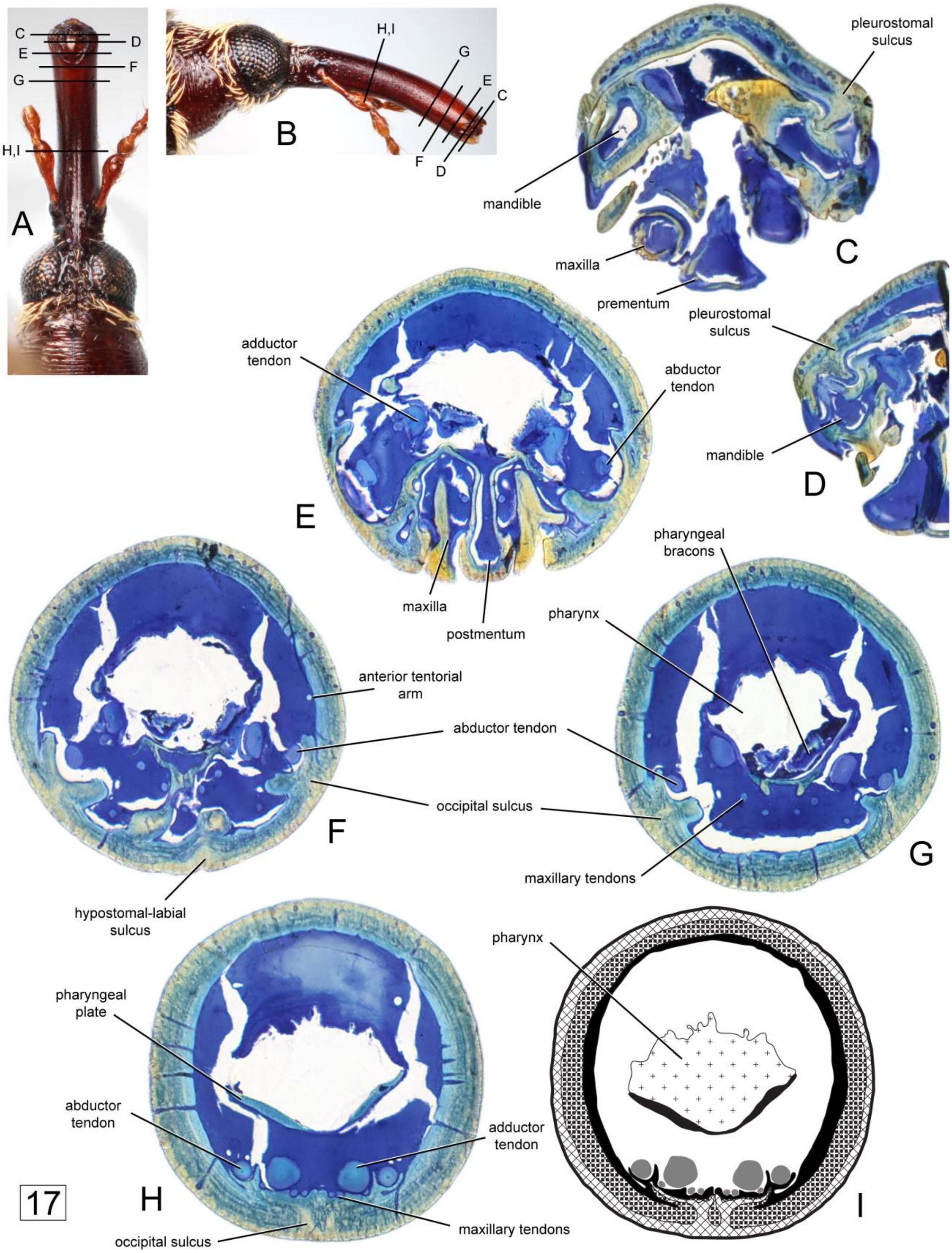
D,F
E
G
G
H
I
anterior condyle
mandible
maxilla
C
anterior tentorial arm
adductor tendon
D
occipital sulcus
abductor tendon
mandible
maxilla
antenna
pharyngeal bracon
prementum
compound eye
antennal socket
anterior tentorial arm
E
occipital sulcus
postmentum
F
adductor tendon
abductor tendon
G
hypostomal sulcus
cerebrum
antennal club
H
gular suture
oesophagous
I
gular suture
14

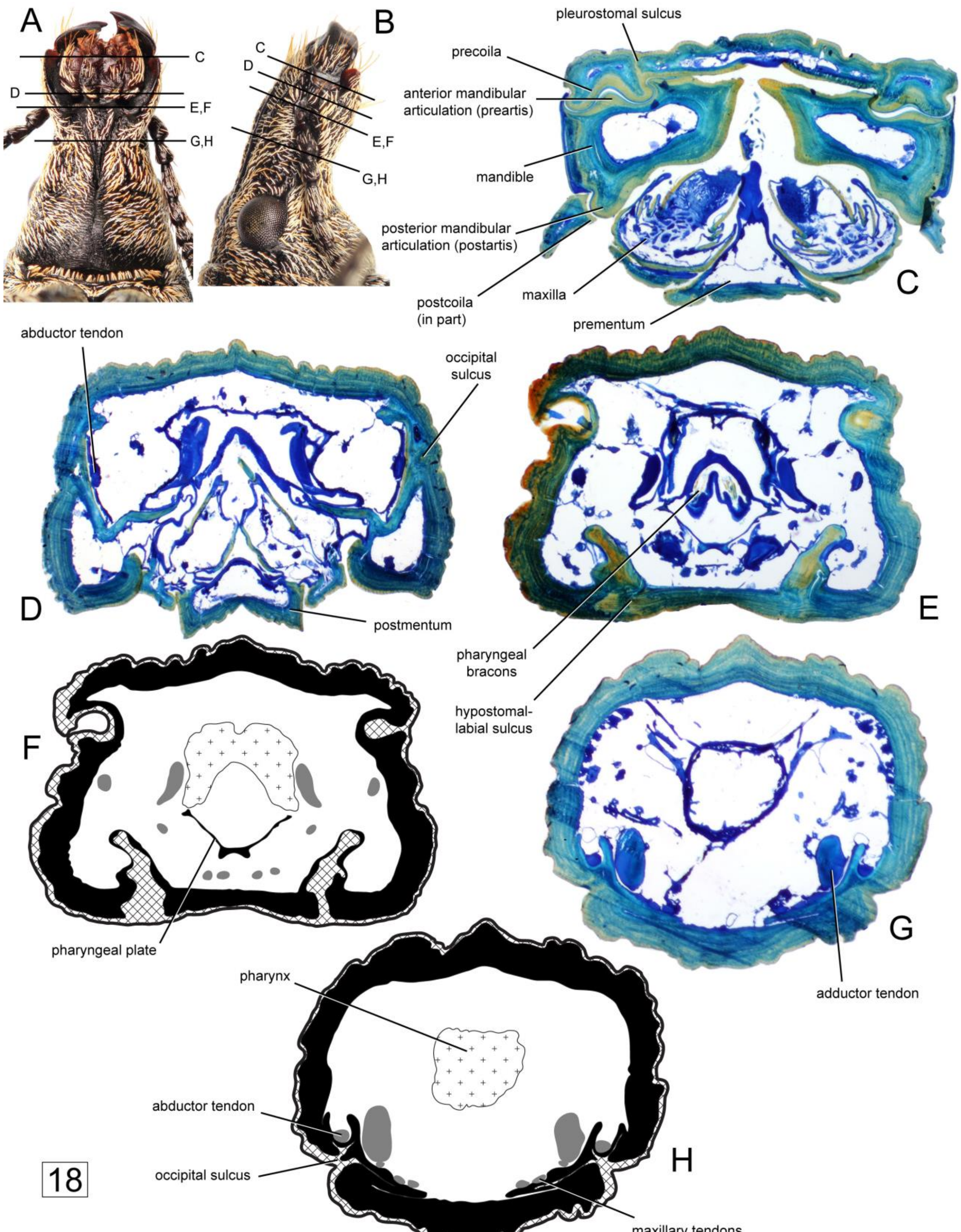

15
A
B
C
D
E
F,H
G
I
J
anterior condyle
pleurostomal sulcus
mandible
maxilla
labium
hypostomal process
prementum
maxilla
anterior tentorial arm
hypostomal-labial sulcus
adductor tendon
abductor tendon
F
occipital sulcus
maxillary tendons
hypostomal-labial sulcus
G
oesophagous
H
hypostomal sulcus
subgenal sulcus
I
hypostomal-labial sulcus
gular suture
J



A
C
D
E,F
G
B
G
E,F
D
C
mandible
C
mandible
maxilla
labium
D
pharyngeal plate
anterior tentorial arm
antenna
E
subgenal sulci
adductor tendon
pharynx
abductor tendon
F
antenna
G
gular suture


16


C
D
E
F
G
H,I
A
B
pleurostomal sulcus
mandible
maxilla
prementum
adductor tendon
abductor tendon
pleurostomal sulcus
mandible
maxilla
postmentum
pharyngeal bracons
pharynx
anterior tentorial arm
abductor tendon
occipital sulcus
maxillary tendons
hypostomal-labial sulcus
pharynx
pharyngeal plate
abductor tendon
adductor tendon
17
occipital sulcus
maxillary tendons
I


A
B
C
D
E,F
G,H
pleurostomal sulcus
precoila
anterior mandibular articulation (preartis)
mandible
posterior mandibular articulation (postartis)
postcoila (in part)
maxilla
prementum
abductor tendon
occipital sulcus
postmentum
pharyngeal bracons
hypostomal-labial sulcus
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F
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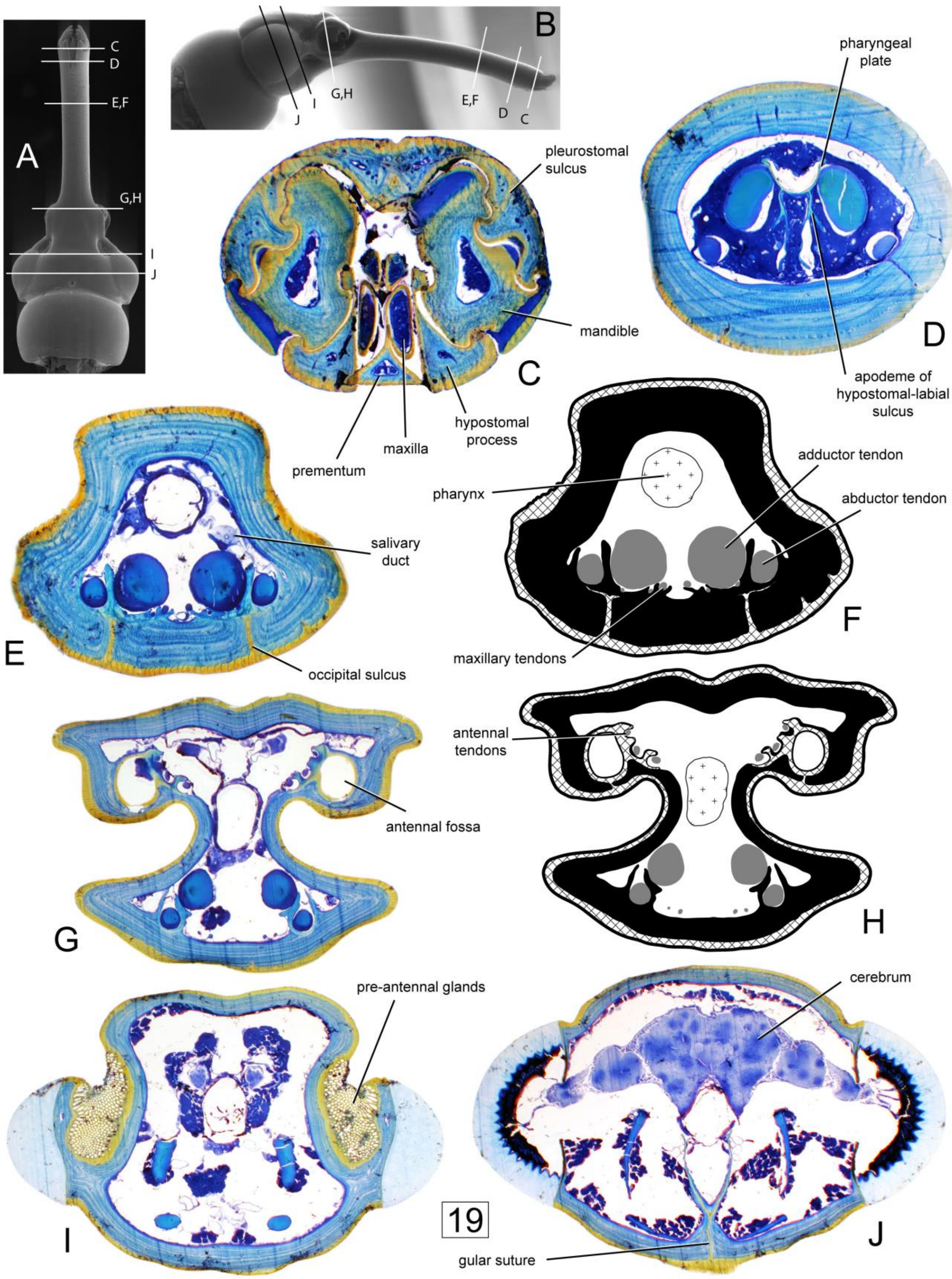
occipital sulcus
H
maxillary tendons
18



A
C
D
E,F
G,H
I
J
B
J
I
G,H
E,F
D
C
pharyngeal plate
pleurostomal sulcus
mandible
C
D
apodeme of hypostomal-labial sulcus
prementum
maxilla
hypostomal process
pharynx
adductor tendon
abductor tendon
salivary duct
E
occipital sulcus
maxillary tendons
F
antennal tendons
antennal fossa
G
H
pre-antennal glands
cerebrum
I
19
J
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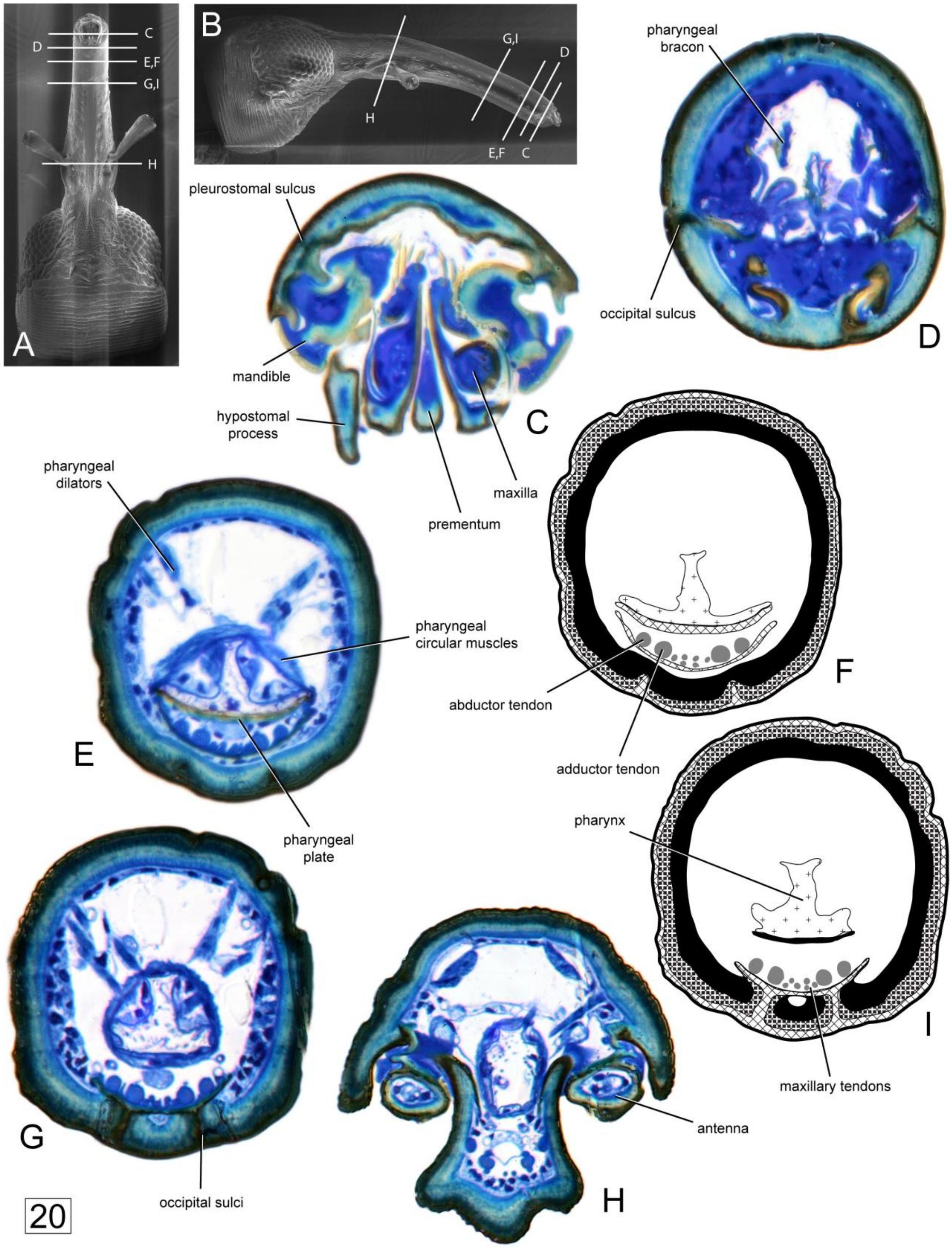
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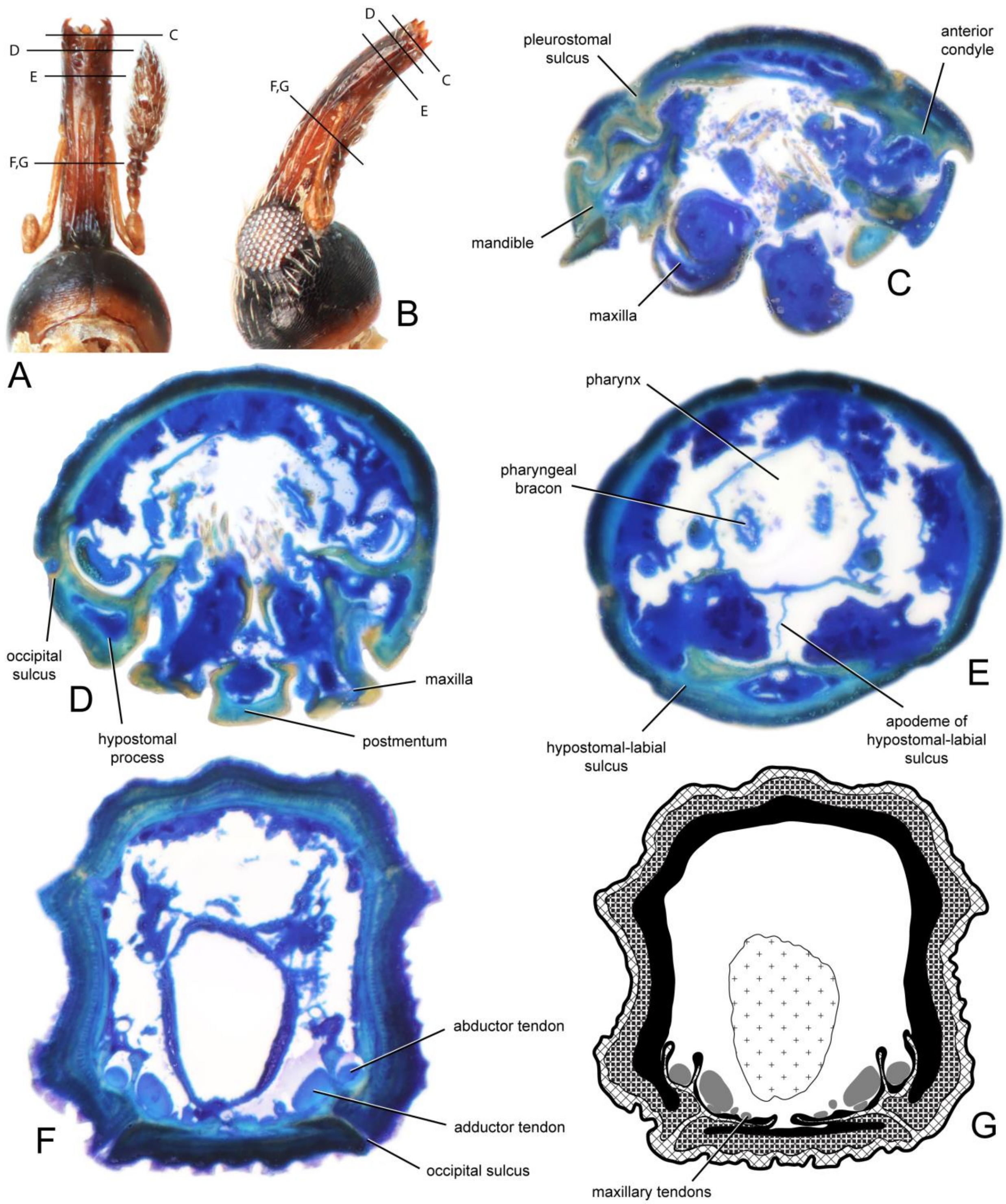
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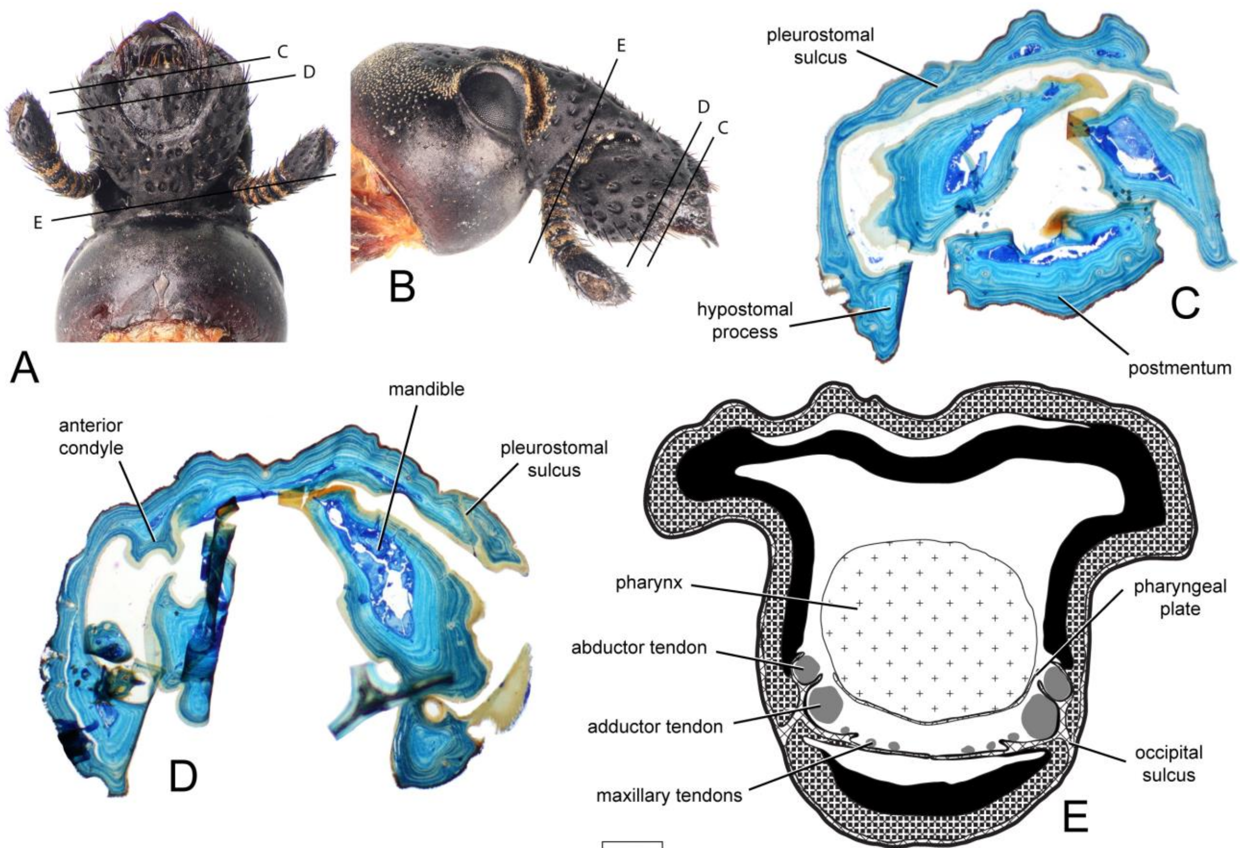
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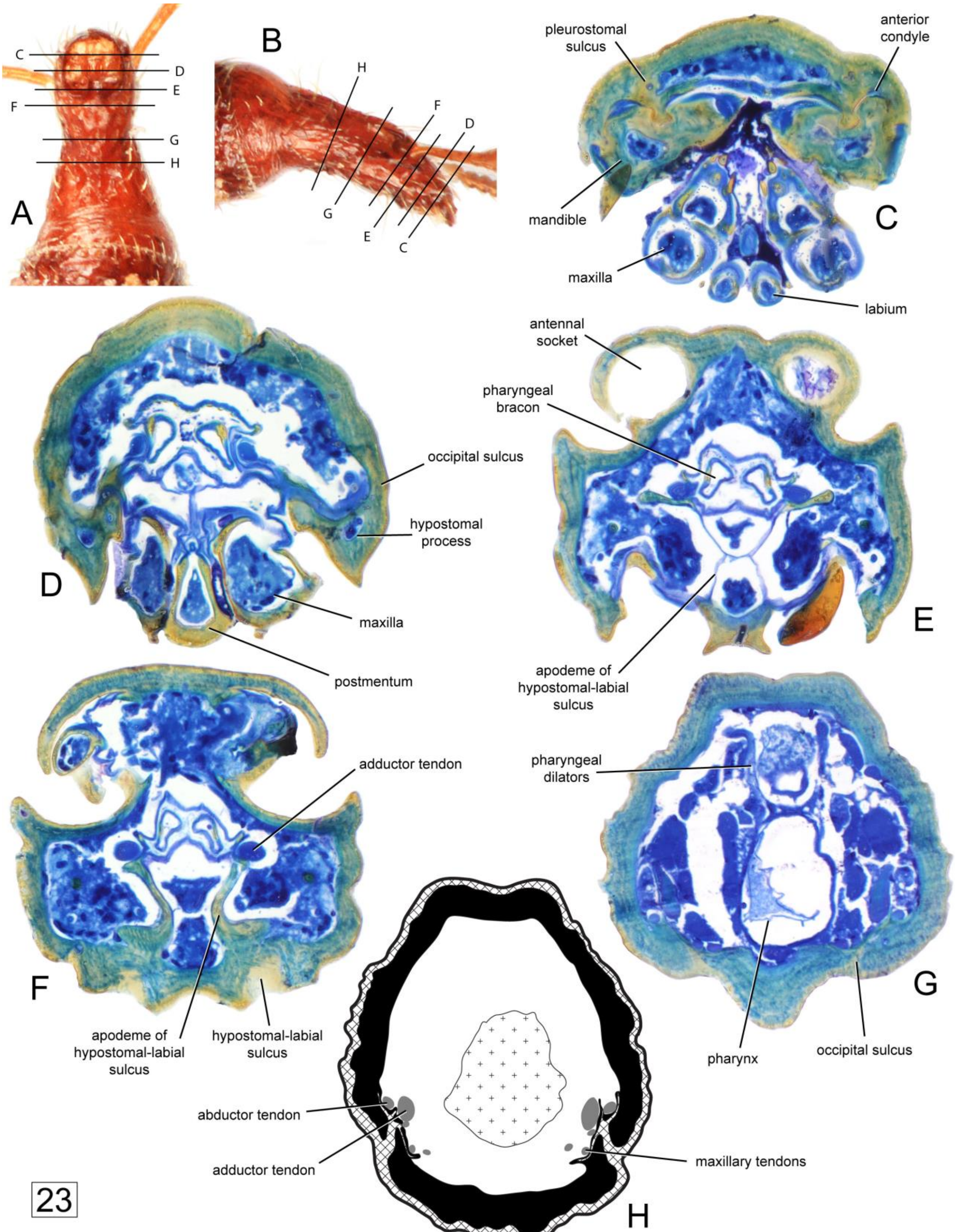

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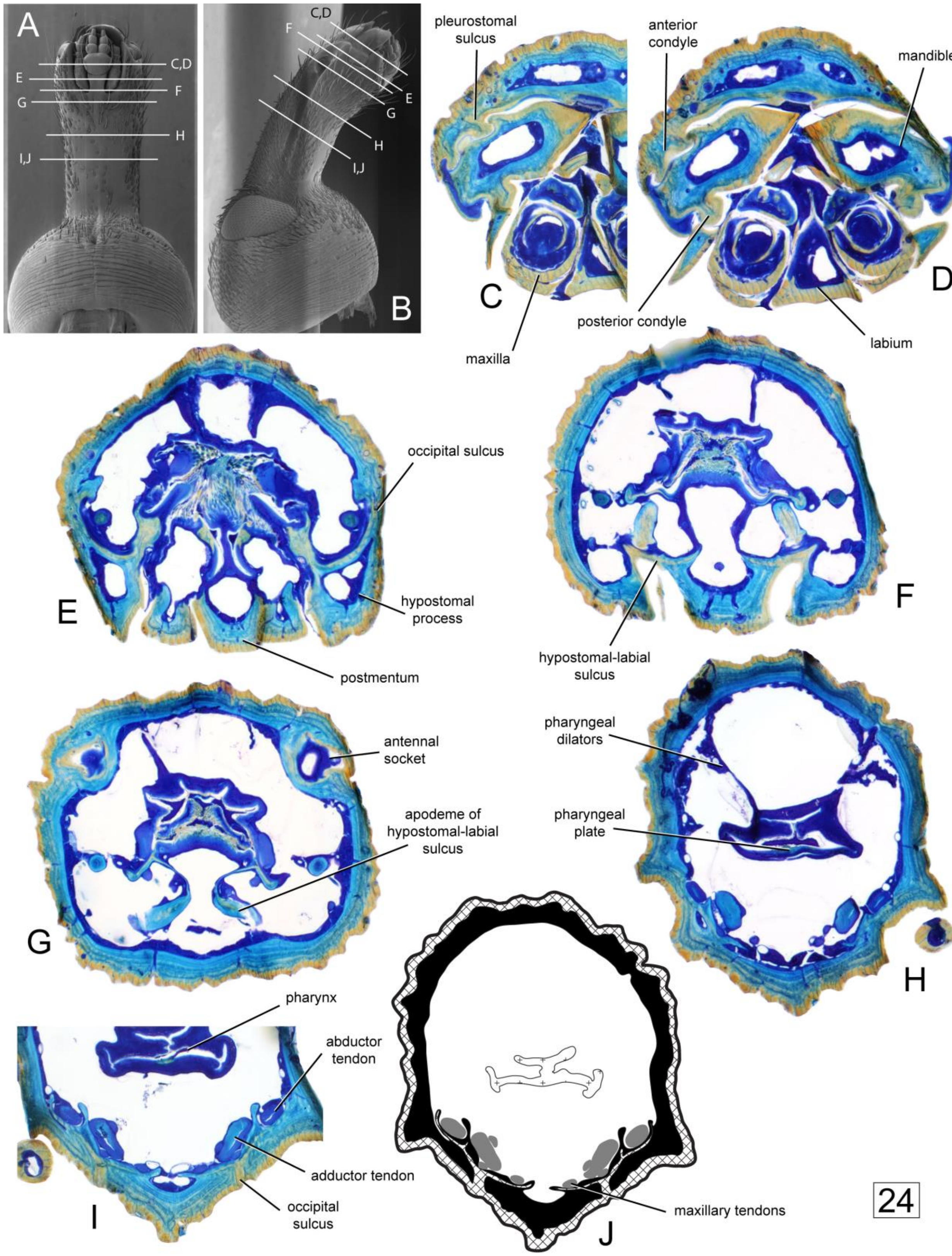

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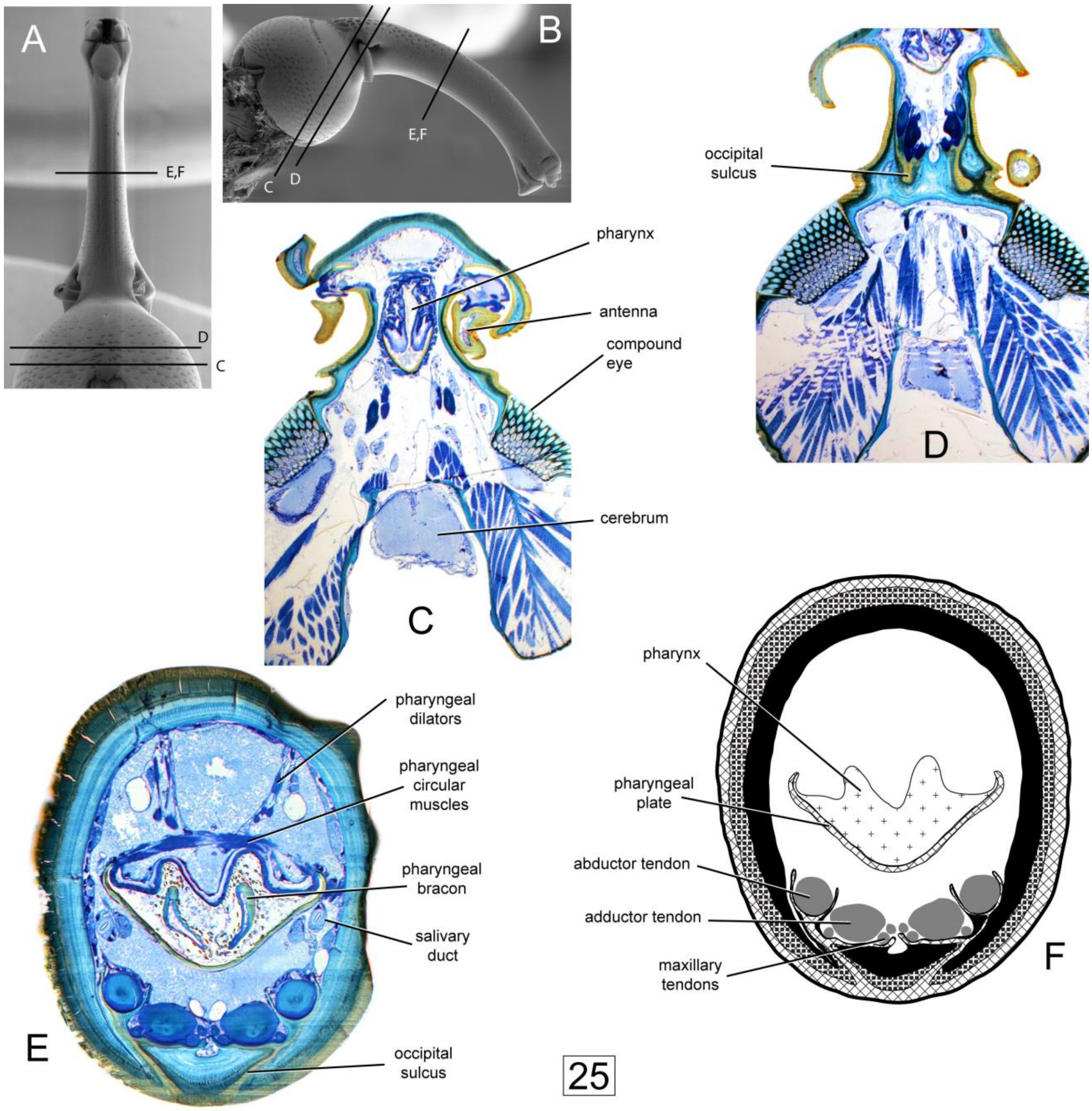
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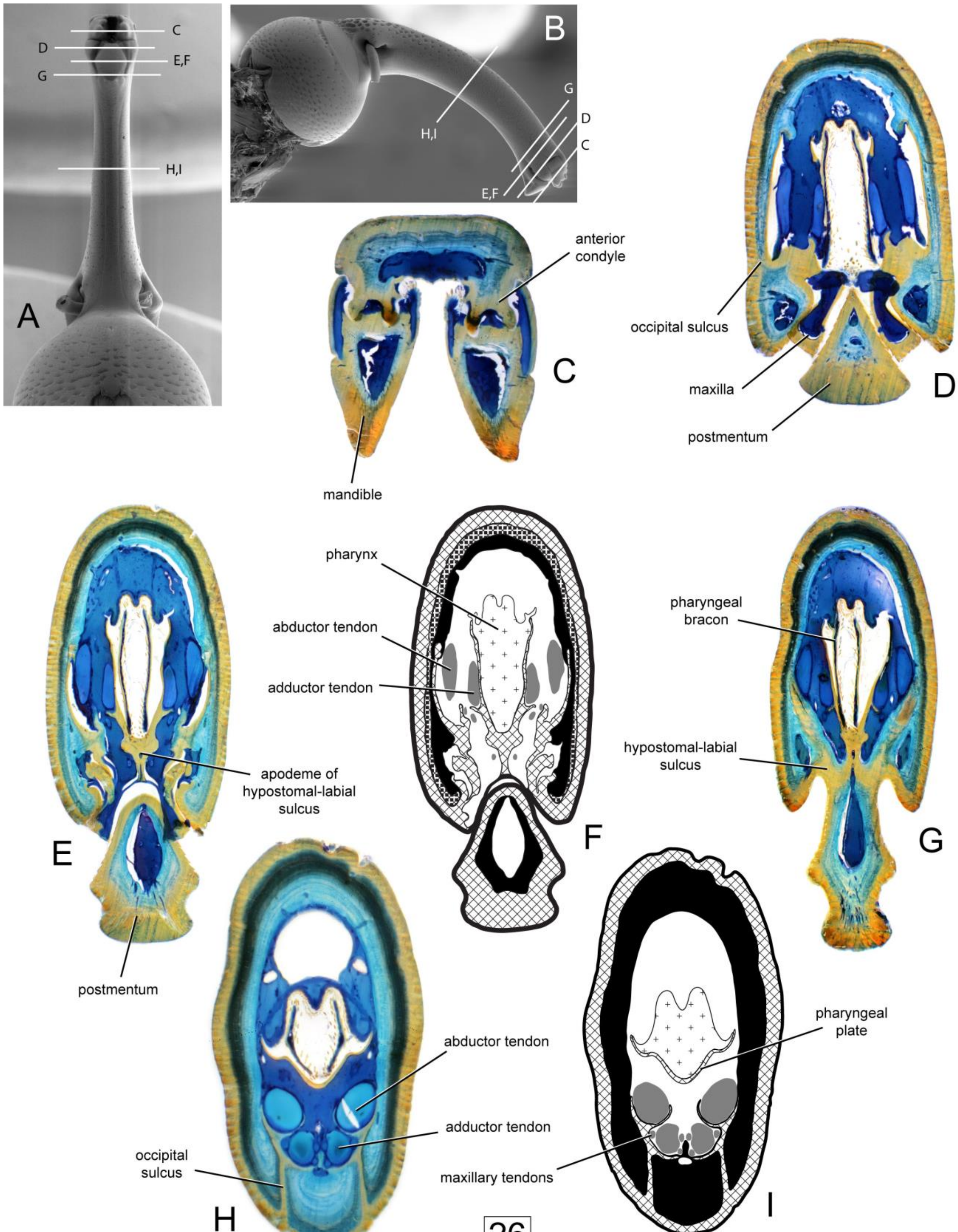

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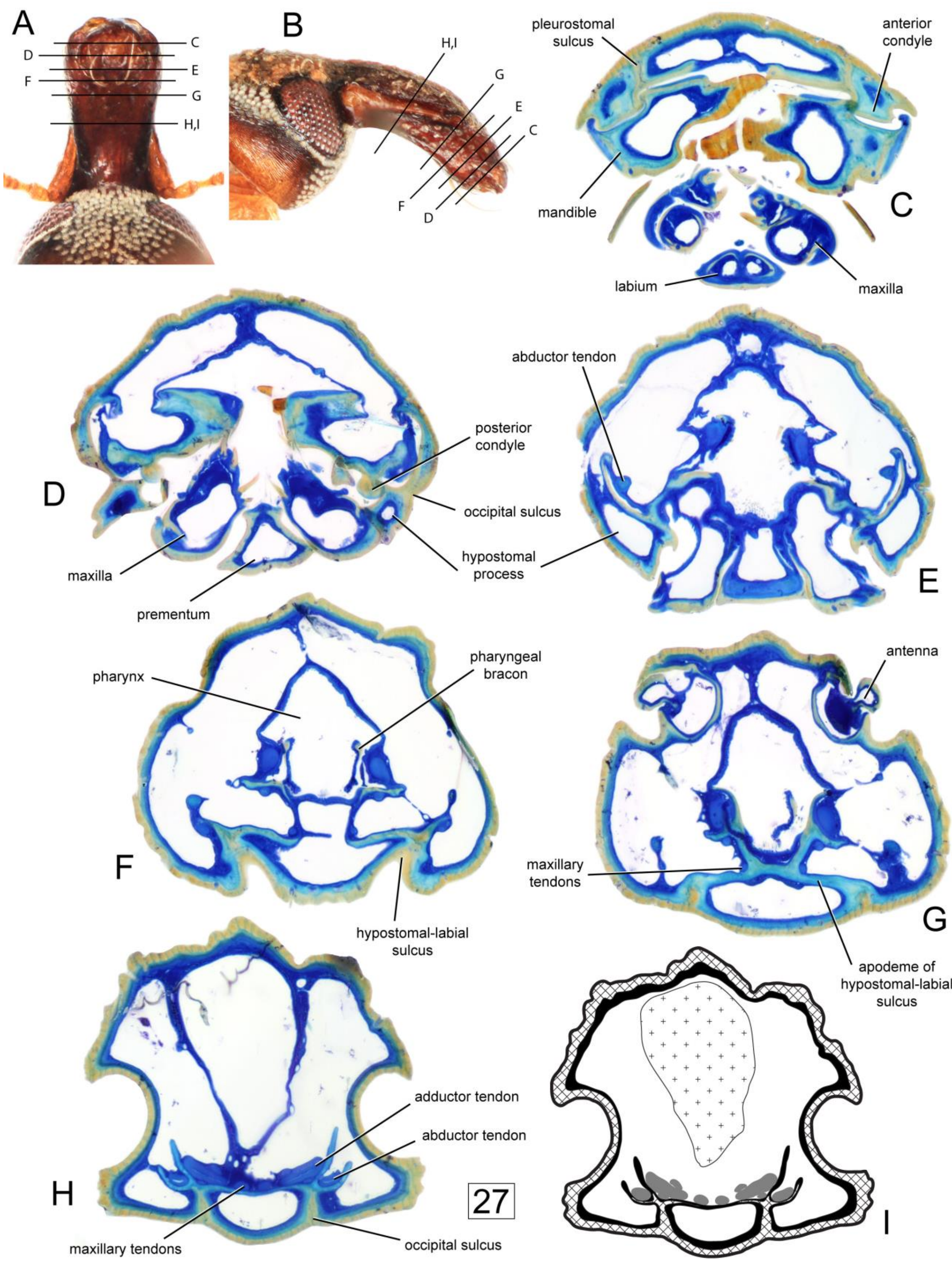
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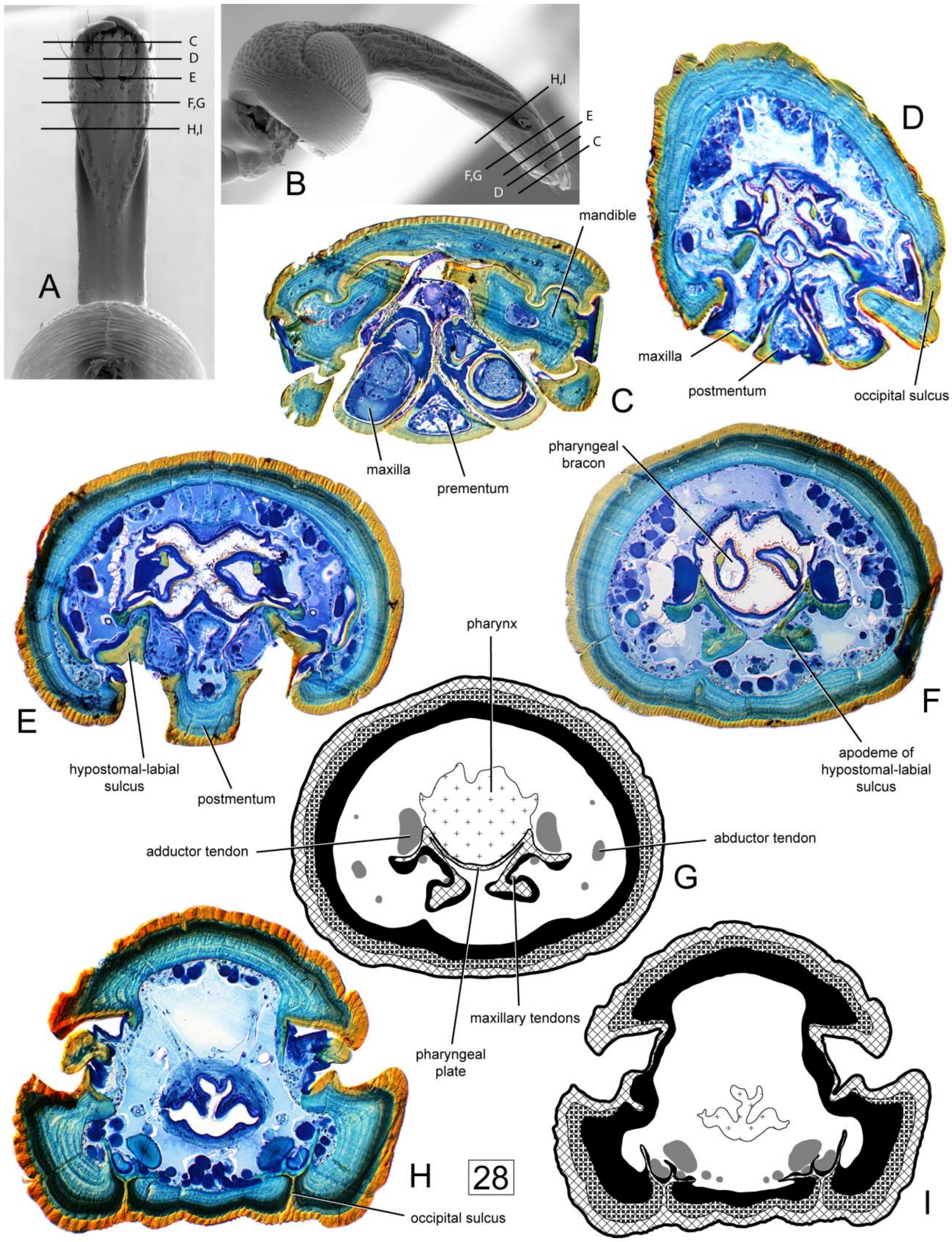

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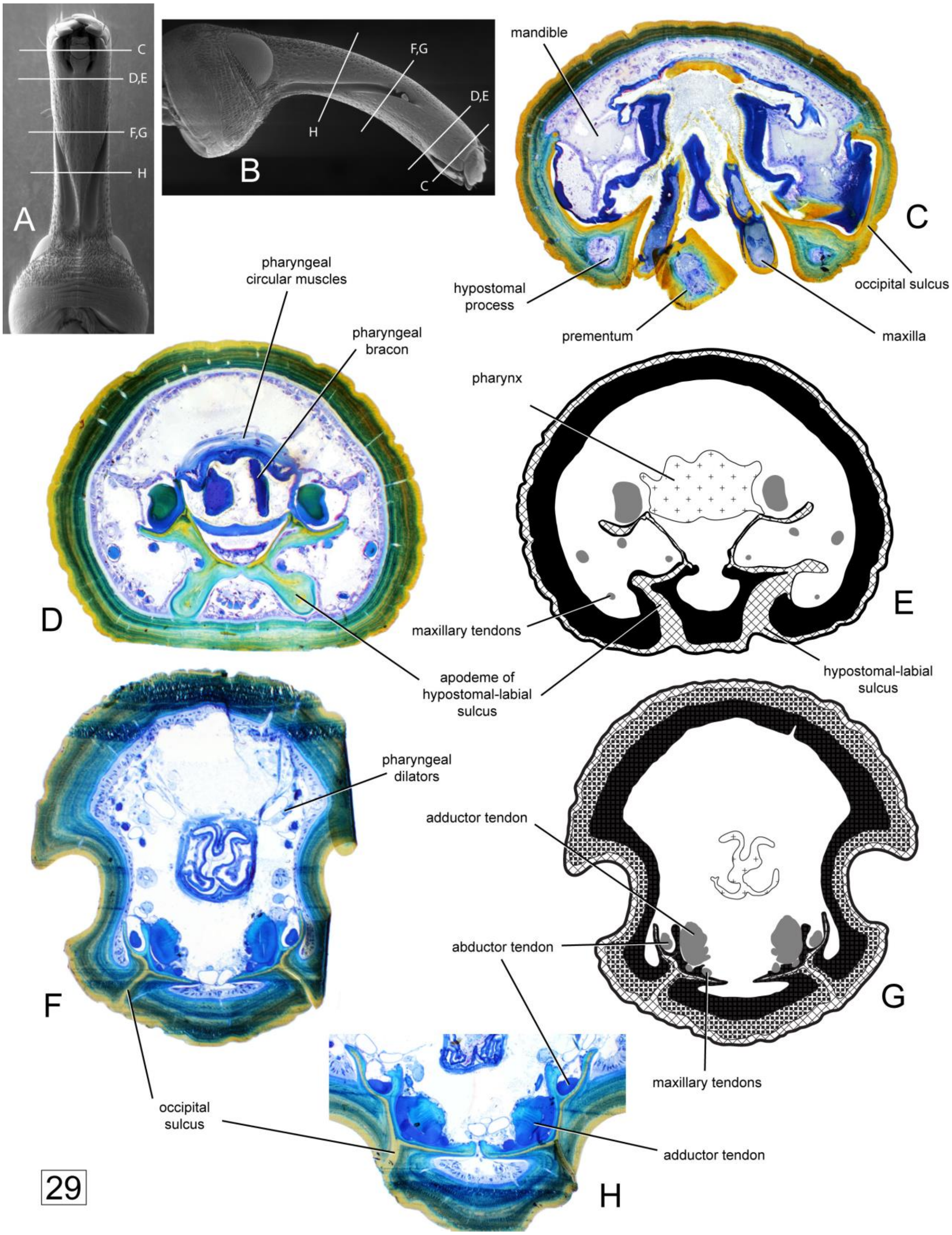
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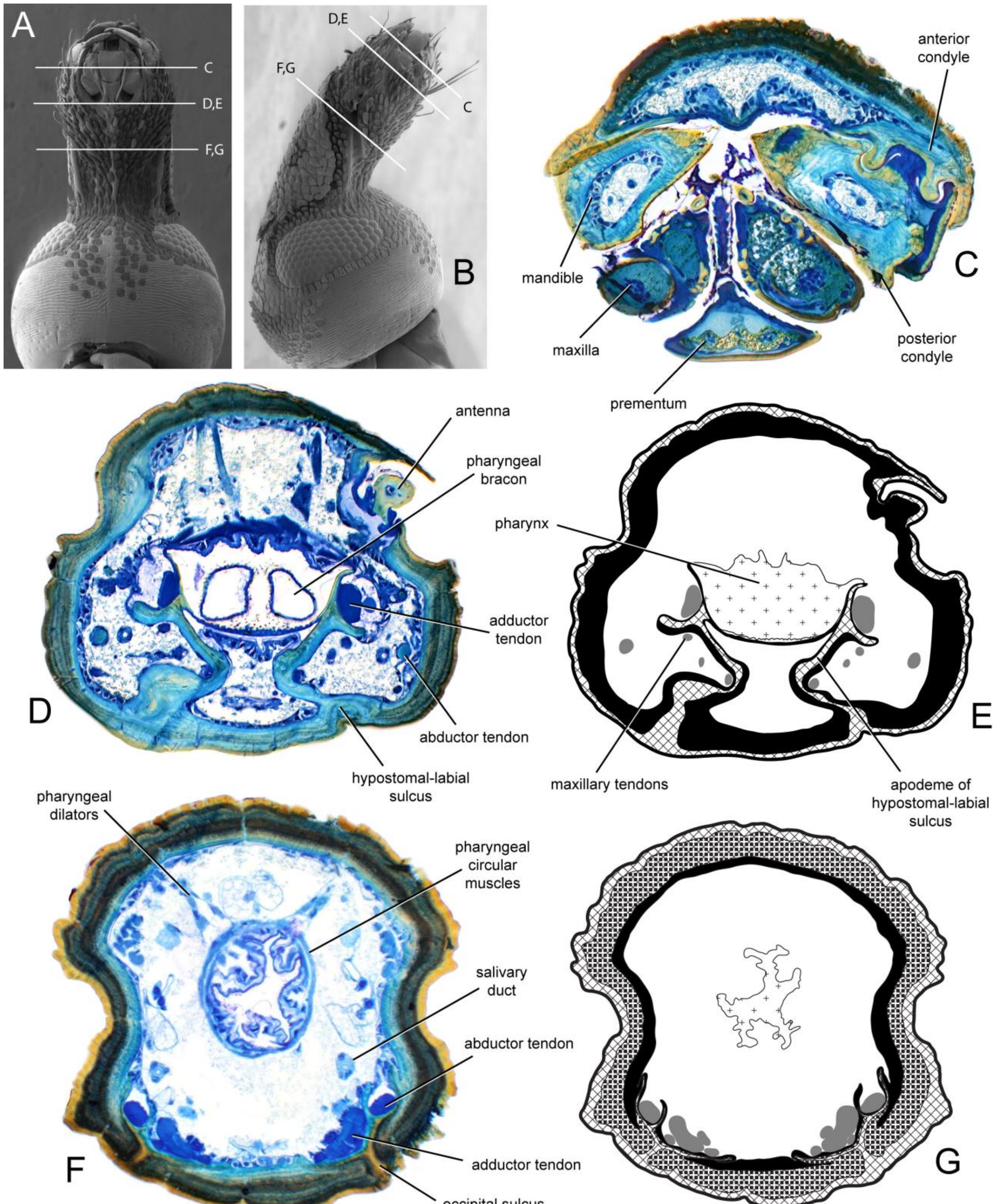

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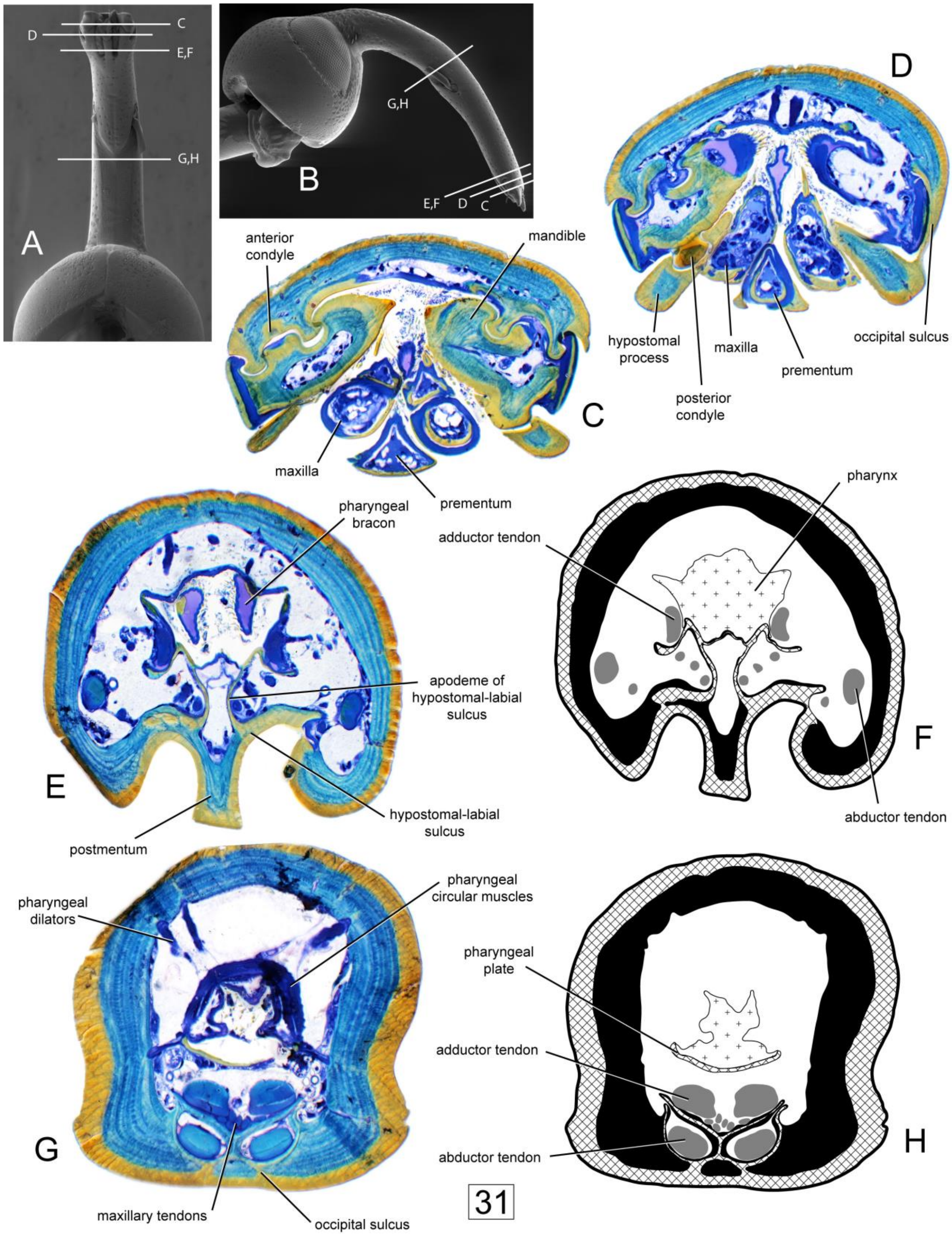
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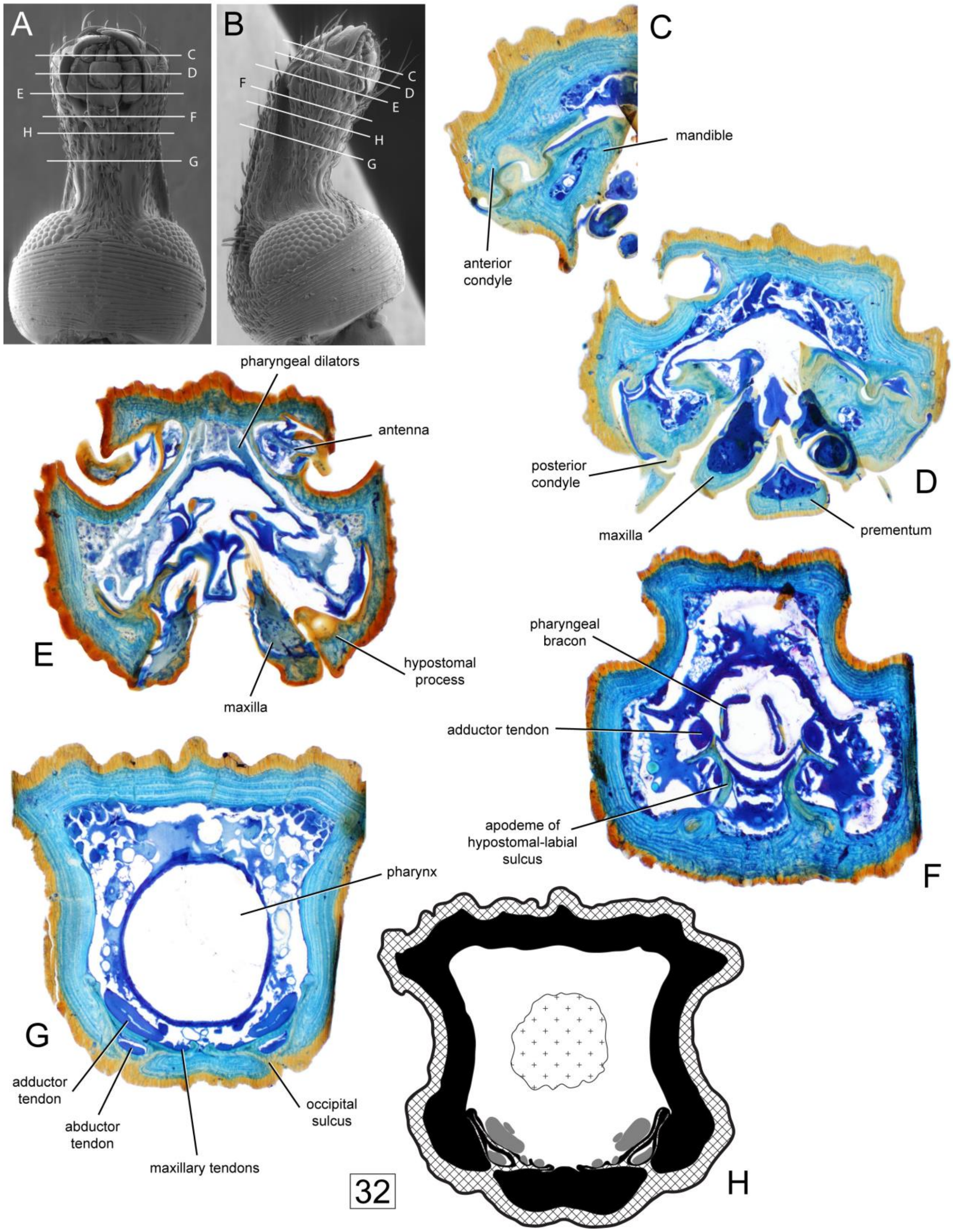

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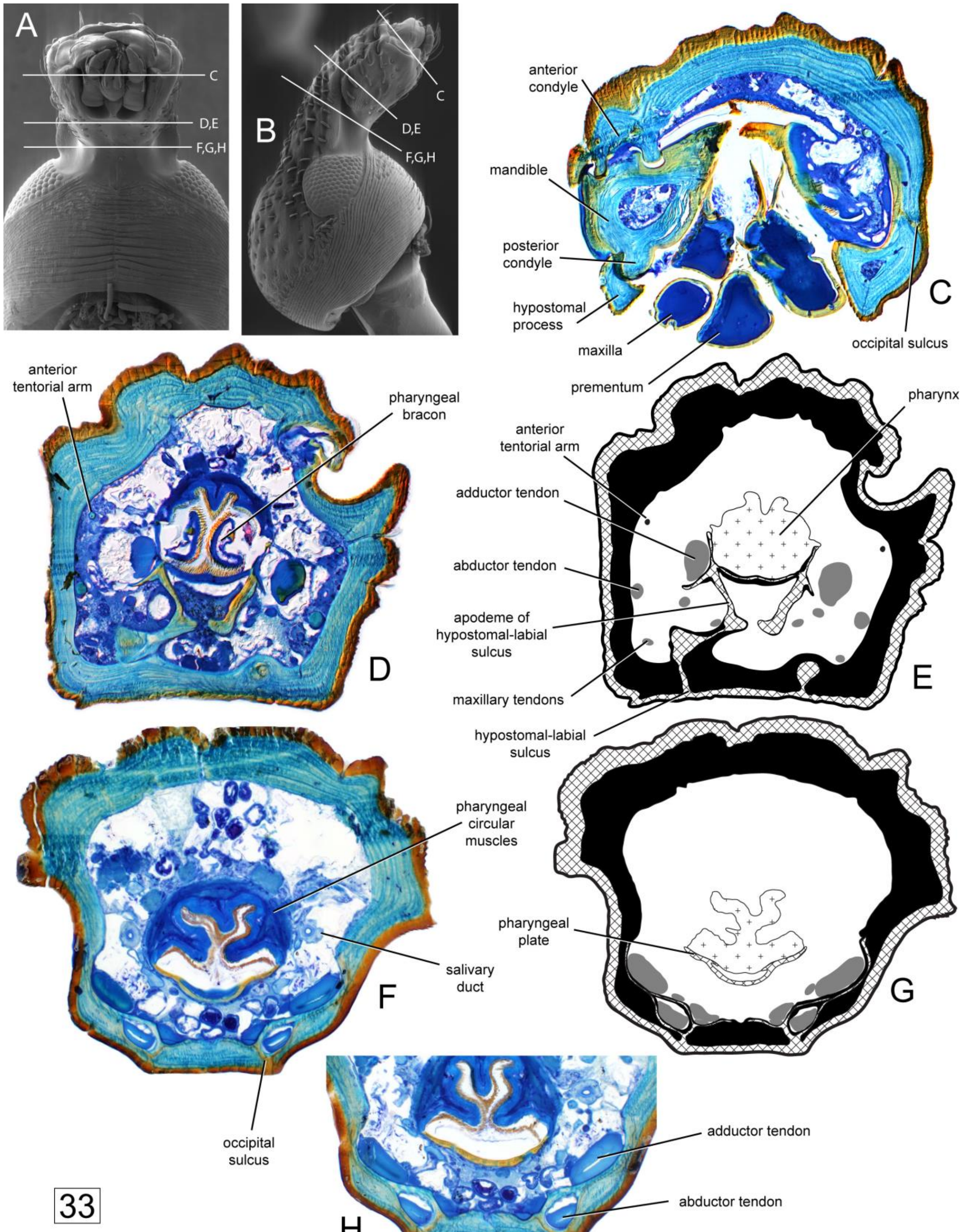

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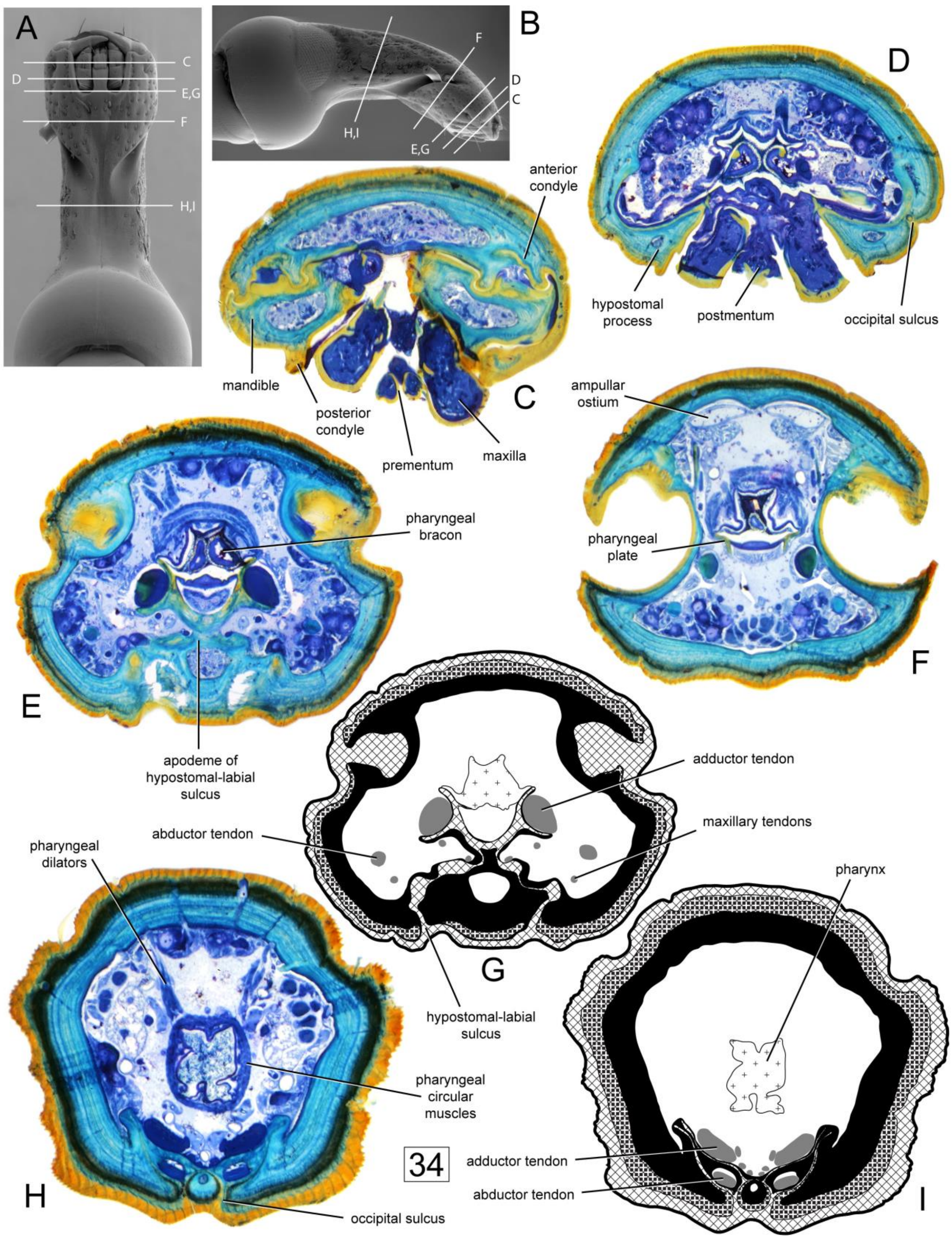
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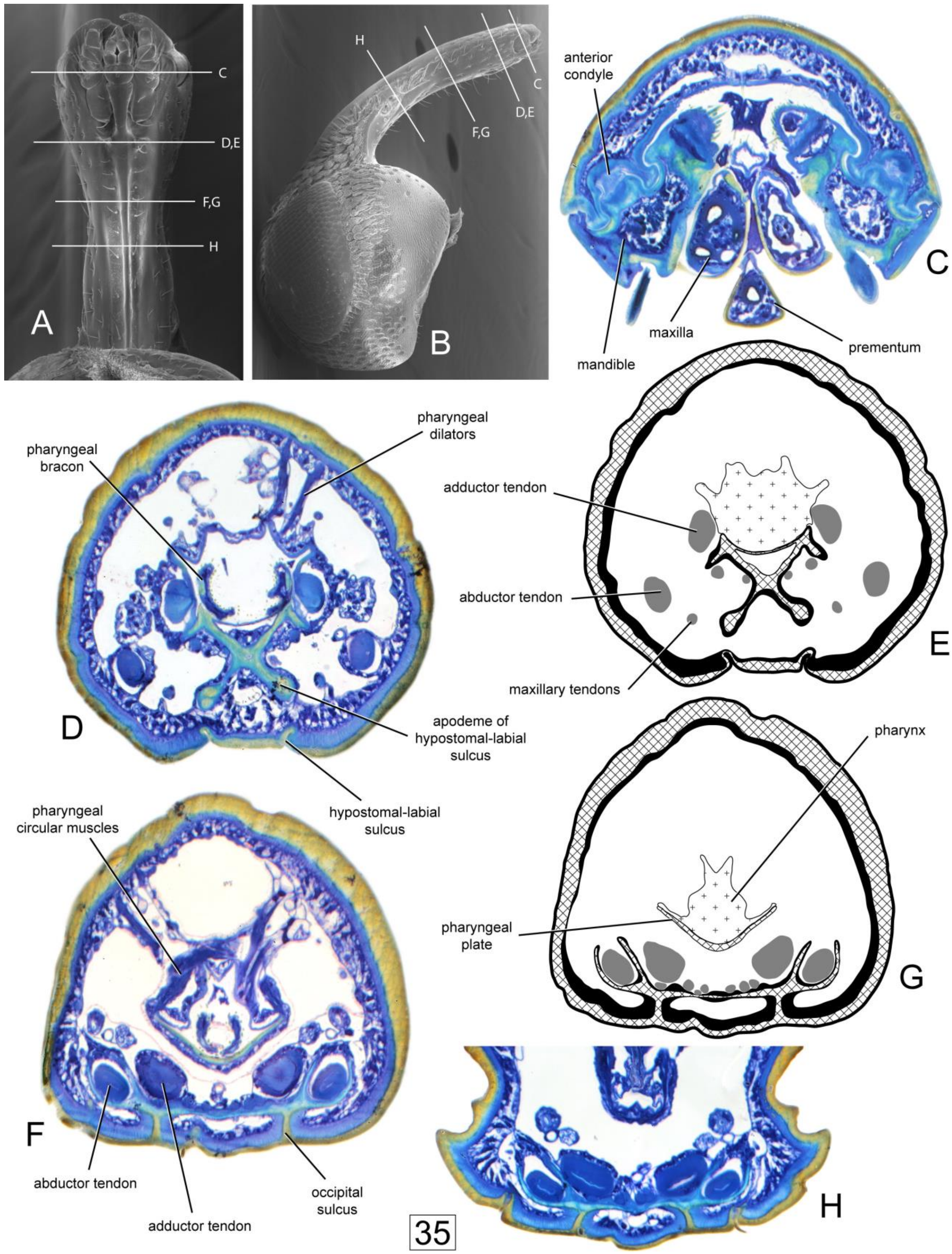
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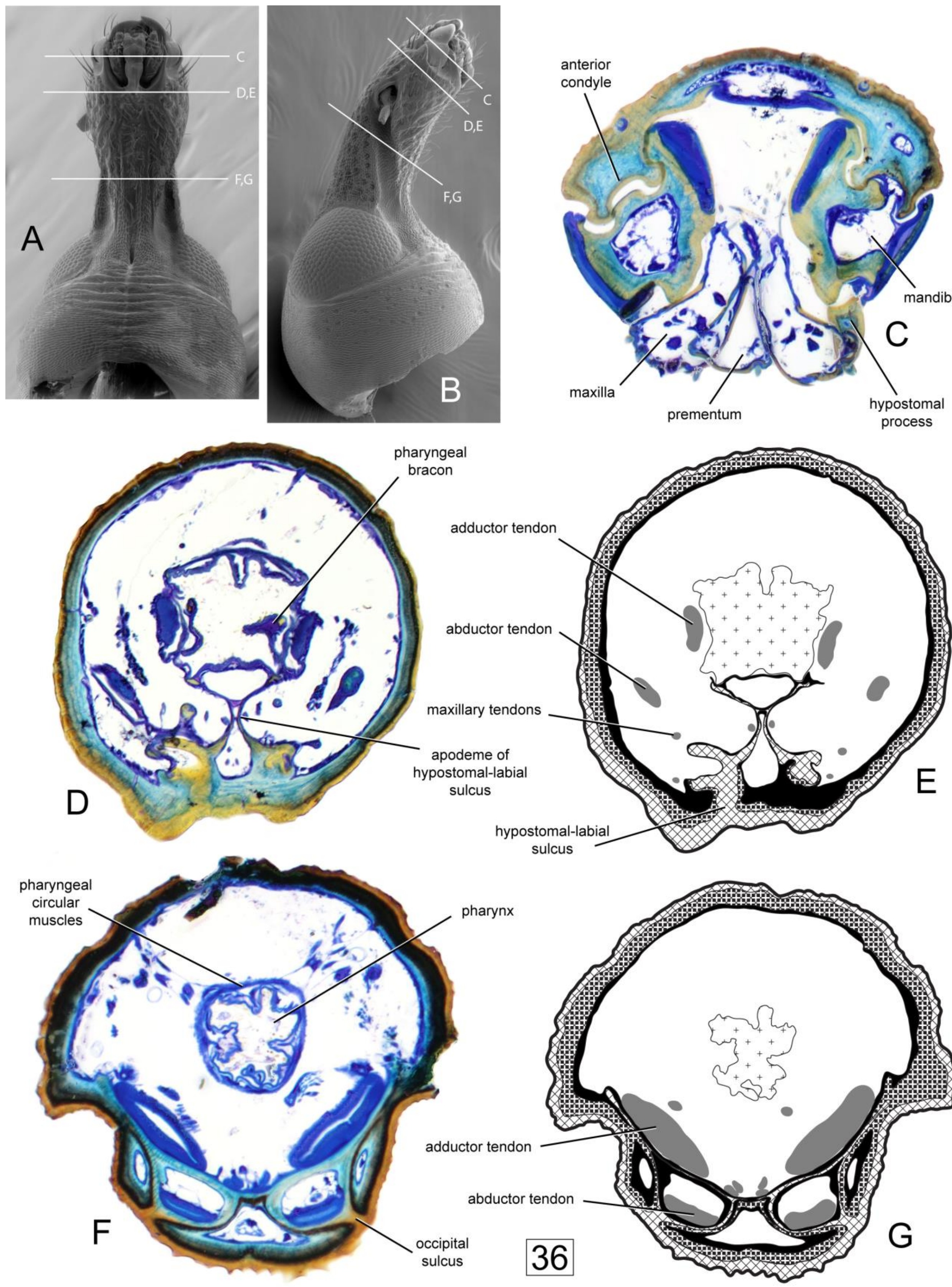
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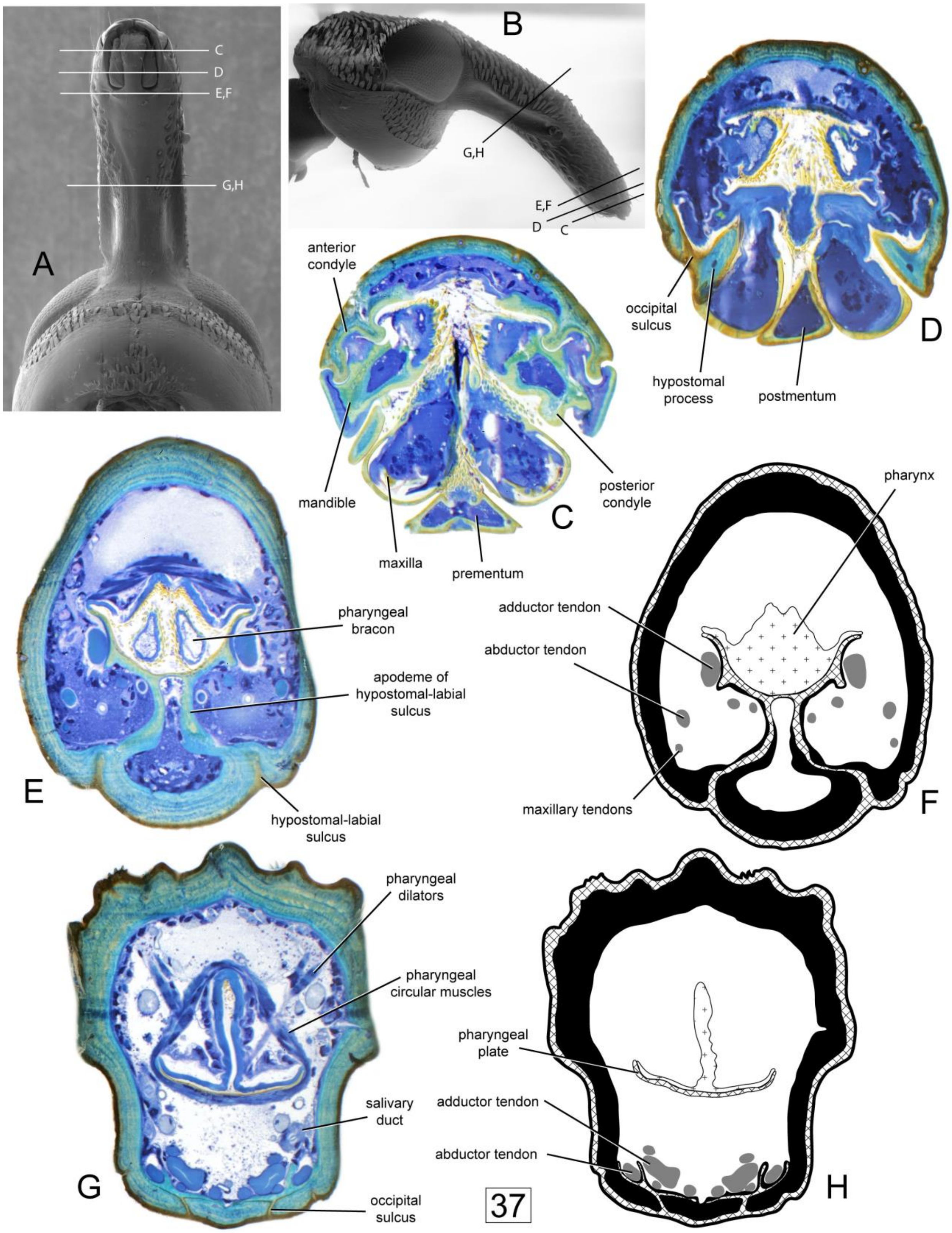
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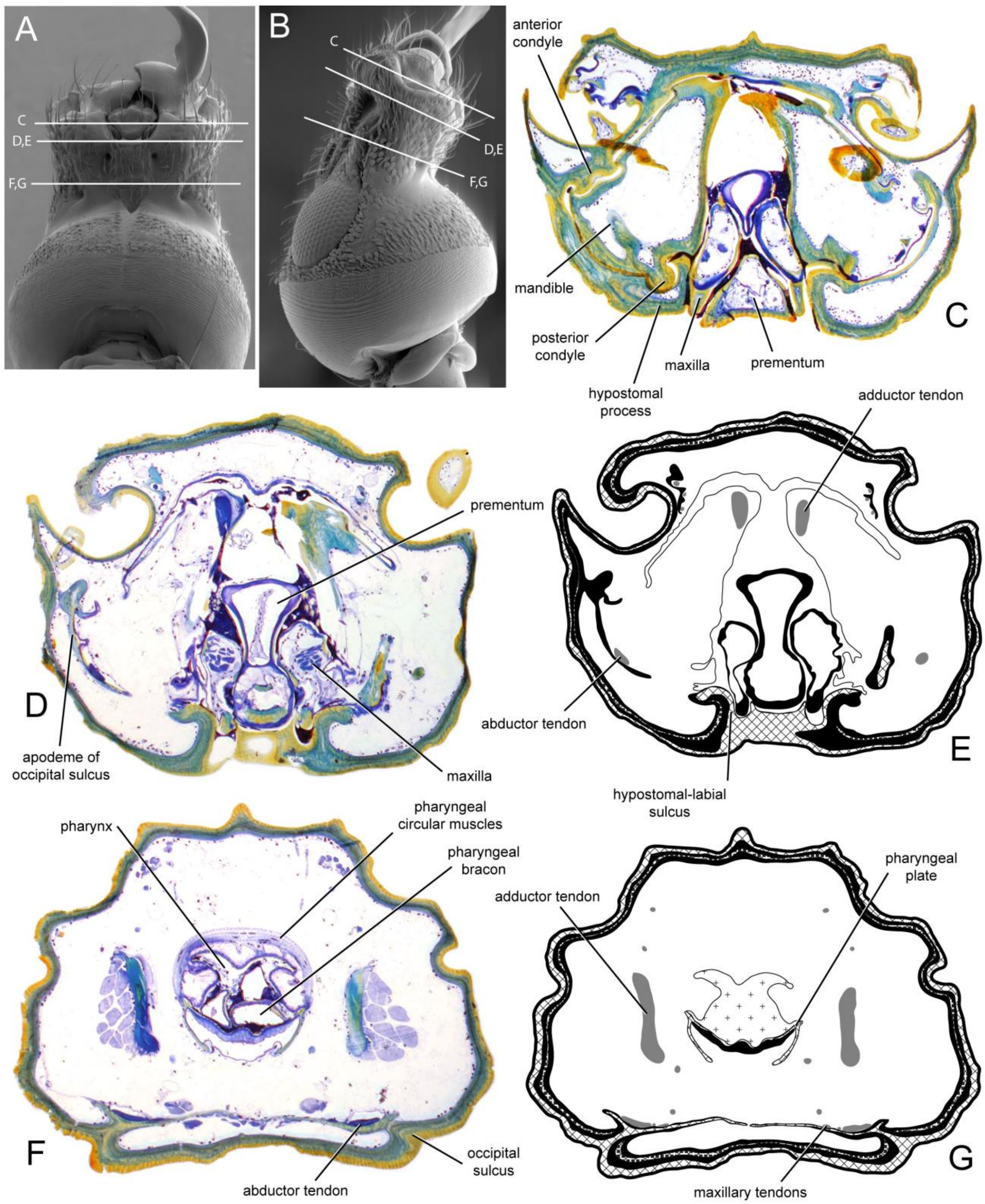
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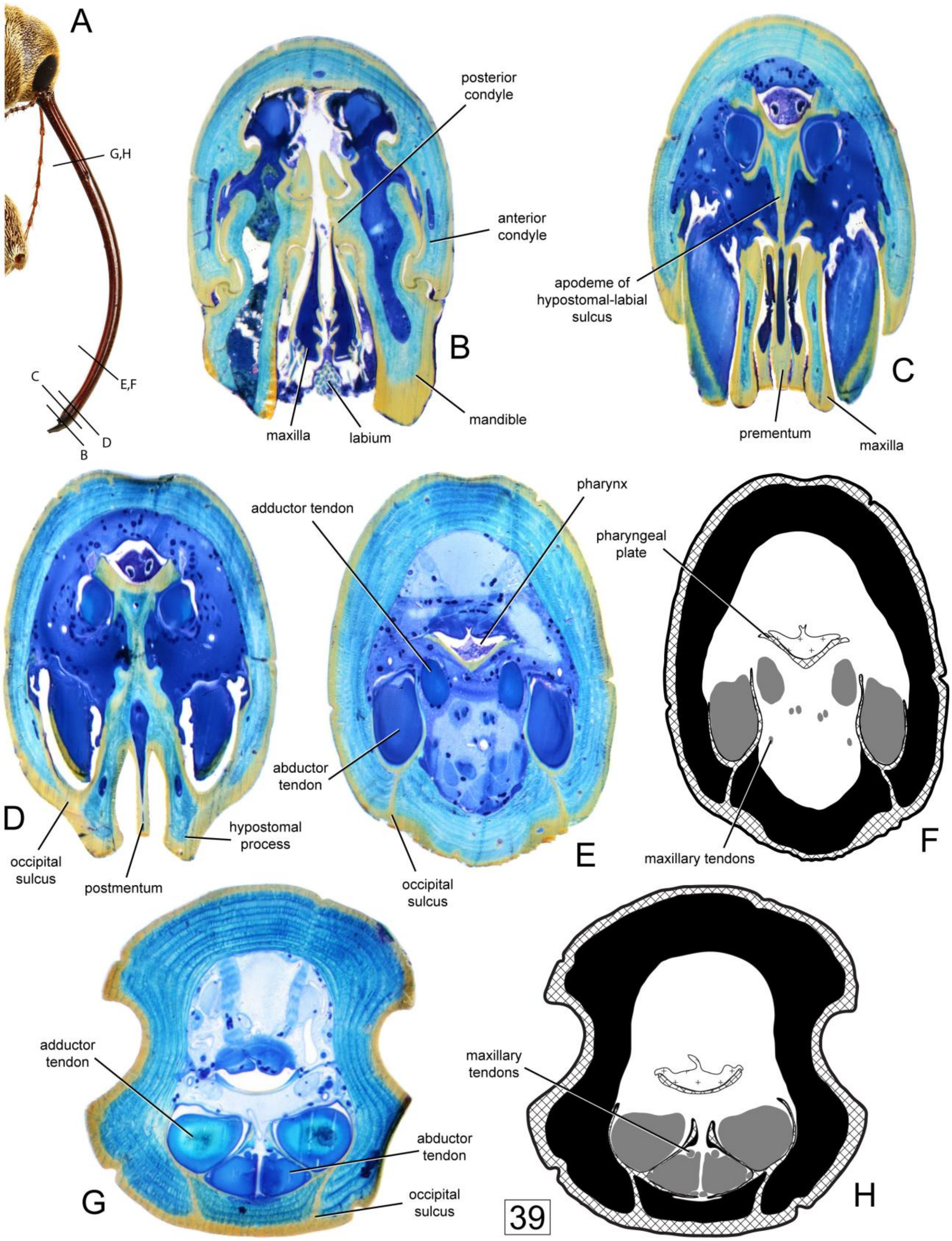
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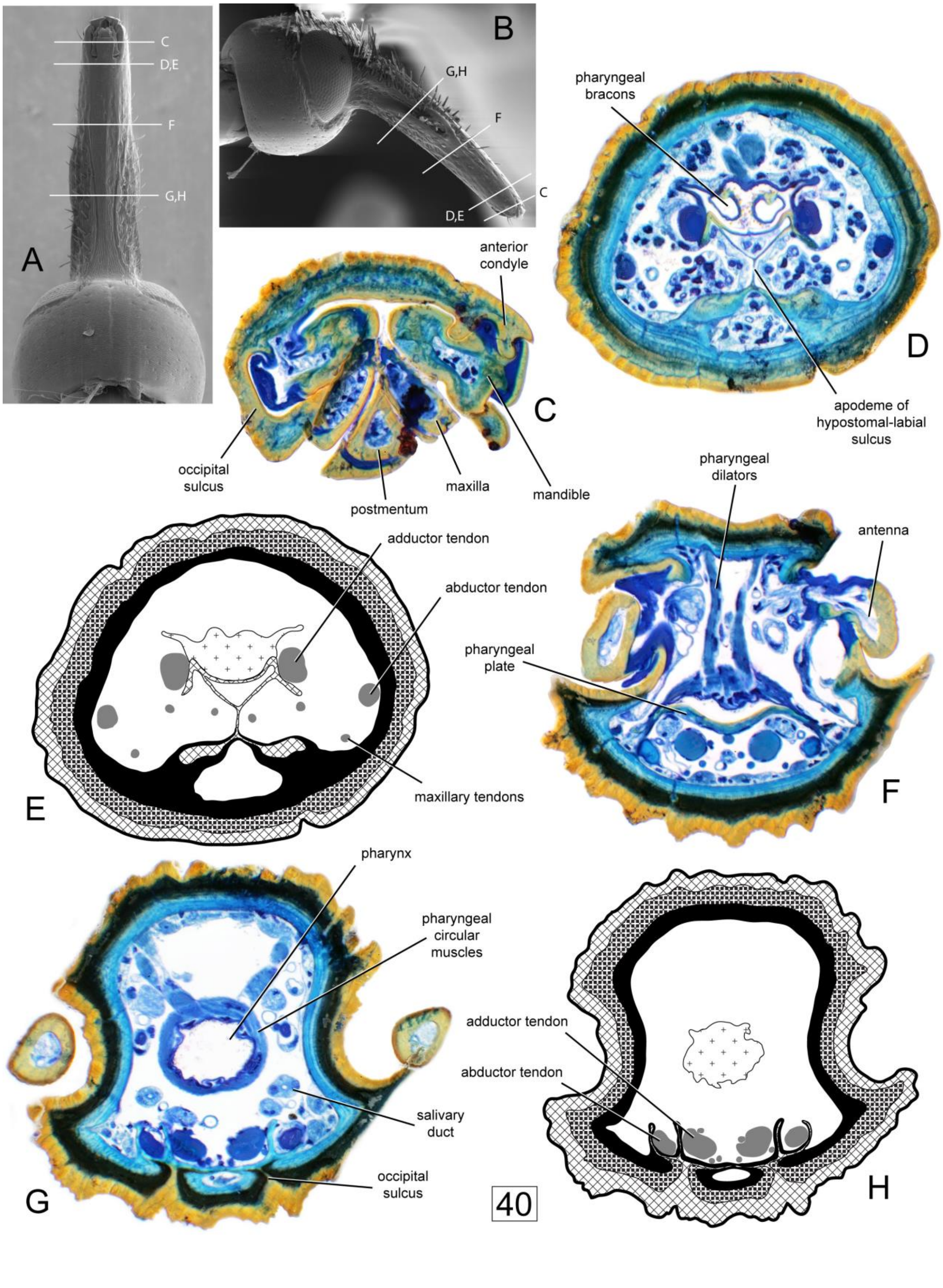
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## 6. Differential gene expression and functional insights in the evolutionary development of the weevil rostrum


### Abstract

The weevil rostrum, for example, is a key evolutionary innovation that has enabled this group to feed on and oviposit in nearly all plant tissues, giving rise to diverse life histories and tremendous diversity in rostrum form. Insights into comparative development of the rostrum will provide insight into the evolution of this key innovation that may be responsible for the explosive radiation of the lineage. Although weevils are an enormous group and countless species are significant agricultural pests, no weevil species have been utilized in developmental studies. In order to better understand the formation and evolution of this structure, transcriptomes from the developing head tissue of 4 weevil species, representing disparate clades and divergent rostral forms, and 1 outgroup (non-weevil species) were generated. While there are difficulties in assessing differences among transcriptomes from divergent taxa, tests for differential expression patterns of transcripts were performed and a refined list of candidate genes has been produced. RNA interference experiments were performed on a subset of candidate genes to test function. This study provided insight into the developmental underpinnings that produced the profound phenotypic diversity observed in the rostrum and the genetic framework that permitted the diversification of such an immense lineage as the weevils.


### Introduction

Weevils (Coleoptera: Curculionoidea) are a diverse group of extant organisms with approximately 50,000 described species. They are of great agricultural significance because they are associated with all major groups of plants and plant tissues. The weevil rostrum, for example, is a key evolutionary innovation that has enabled this group to feed on and oviposit in nearly all plant tissues, giving rise to diverse life histories and tremendous diversity in rostrum form (Fig. 1). Studies into comparative development of the rostrum will provide insight into the evolution of this key innovation that may be responsible for the explosive radiation of the lineage (Anderson 1995, Oberprieler *et al.* 2007). In beetles (Coleoptera), *Tribolium* (Tenebrionidae) has been the primary model in which to study evolutionary developmental mechanisms (e.g., Tomoyasu *et al.* 2005). An exciting and relatively recent addition is a species of *Onthophagus* (Scarabaeidae), which has emerged as a new model for examination of horn development (Moczek and Nagy 2005; Moczek and Rose 2009; Moczek *et al.* 2006, 2007). Although weevils are an enormous group and countless species are significant agricultural pests, no weevil species have been utilized in developmental studies.

From previous morphological and histological observations (Davis 2011), patterning of the adult rostrum begins in the early 4$^{th}$ instar larva and continues throughout the pupal stage. Rostrum formation may combine genetic elements of appendage development and segment patterning and identity; aside from adult appendage patterning, however, relatively little research has focused on the formation of adult structures. Also, because head segmentation is established beginning in the embryo, the majority of research has traditionally focused on these early stages to understand developmental pathways. Because the rostrum is composed of several head segments, though the demarcation of which is uncertain, these segments may be delimited posteriorly with the homeodomain segment polarity gene *engrailed* (*en*), which is known to specify posterior segment boundaries in *Drosophila* and *Tribolium* (Rogers and Kaufman 1996; Schmidt-Ott and Technau 1992; Schmidt-Ott *et al.* 1994). Also, since the rostrum appears to be formed from the elongation of different combinations of these segments, the appendage patterning gene *distal-less* (*dll*) may also be a prime candidate for examining this pattern, as it has been shown to initiate secondary axes in the limbs of all arthropods (Panganiban and Rubenstein 2002; Panganiban *et al.* 1994, 1997). Other genes that may be hypothesized to be of importance, are the segment polarity gene *wingless* (*wg*), the homeotic selector genes *labial* (*lab*), *proboscipedia* (*pb*), and *deformed* (*dfd*) (Diederich *et al.* 1991), which are part of the Antennapedia complex, and the appendage patterning gene *dachshund* (*dac*).

In order to better understand the formation and evolution of this structure, transcriptomes from the developing head tissue of 4 weevil species, representing disparate clades and divergent rostral forms (Figs. 2-6), and 1 outgroup (non-weevil species) were produced in *de novo* assemblies. While there are difficulties in assessing differences among transcriptomes from divergent taxa, tests for differential expression patterns of transcripts were performed to characterize differences in the gene networks that have produced the profound phenotypic diversity observed in the rostrum and to better understand the genetic framework that permitted the diversification of such an immense lineage as the weevils. Functional tests of candidate genes were performed through RNAi, in which the gene of interest is silenced by injecting double-stranded RNA into the posterior end of the larva (in the case of beetles) and the mutant phenotype documented.

**Methods**

Pre-pupae (pharate pupae) were obtained for 5 species: 4 weevil species (*Dendroctonus ponderosae* (Fig. 3), *Sitophilus oryzae* (Fig. 4), *Curculio pardalis* (Fig. 5), *Diaprepes abbreviatus* (Fig. 6)) and 1 outgroup (Chrysomelidae: Bruchinae: *Callosobruchus maculatus*;

Fig. 2), and pupae were also obtained for *S. oryzae*. Frozen specimens were decapitated and the RNA extracted using Trizol and standard protocols. Library preparation followed the Illumina TruSeq protocol (low-throughput), incorporating Covaris shearing as an alternative to chemical shearing and excluding the cDNA DSN Normalization step. Illumina 100bp, paired-end, RNAseq sequencing was performed at the University of Kansas Medical Center Genome Sequencing Facility on a HiSeq2000 platform. Transcriptome assemblies were performed *de novo* using Trinity (Fig. 7). Blast2GO® V.2.5.1 (Conesa *et al.* 2005; Conesa and Götz 2008; Götz 2008, 2011) and NCBI Blast 2.2.25+ (Altschul *et al.* 1990) were used to obtain transcript identities and gene ontology terms. A combination of RSEM 1.1.17 (Li and Dewey 2011) and EdgeR (McCarthy *et al.* 2012; Robinson and Oshlack 2010; Robinson *et al.* 2010; Bioconductor: Gentleman *et al.* 2004), and Bowtie2 (Langmead and Salzberg 2012) and DESeq (Anders and Huber 2010; Bioconductor: Gentleman *et al.* 2004) were used to map raw reads onto the *S. oryzae* transcriptome, obtain a counts table of the mappings, and identify transcripts that are significantly differentially expressed at a 10% false discovery rate between *D. ponderosae* and *S. oryzae*. The resulting transcripts identified as differentially expressed were subsequently submitted to Blast 2.2.25+ and Blast2GO®. A comprehensive transcriptome of *S. oryzae* was also produced by combining the pupal and prepupal transcripts, in which subsequent analyses of differential expression were performed between the prepupal and pupal stages. In attempting to perform all pairwise comparisons of differential expression among the 5 exemplar taxa, the most suitable pairs were *D. ponderosae* + *S. oryzae* and *D. abbreviatus* + *C. maculatus*. This determination is derived from the percentage of raw sequence reads that map onto the transcriptome of the other taxon in the pair.

RNA interference (RNAi) was performed to create loss-of-function phenotypes following the *Tribolium* protocols of Tomoyasu and Denell (2004) and Tomoyasu *et al.* (2005, 2009). To produce dsRNA, the PCR product of the gene of interest was cloned using the TOPO® TA cloning® kit for sequencing and utilizing One Shot® TOP10 chemically competent *E. coli*. T3/T7 primers were then used for PCR reactions to obtain the insert sequence and dsRNA produced with the MEGAscript® T7 kit. In order to visualize the dsRNA, approximately 0.5 µL of green food coloring was mixed with 14 µL of dsRNA solution in distilled water. To produce a strong phenotype, a concentration of at least 1 µg/µL of dsRNA was required, injecting approximately 0.5-1 µL into each larva. The last larval instar ($4^{th}$ instar, before the prepupal stage) was injected with dsDNA and the adult phenotypes were observed.

**Results**

Sequencing using the Illumina platform yielded a total of 304,996,599 100bp reads (forward and reverse reads combined) for *S. oryzae*. The total number of assembled contigs was 59,972, of which 27,937 were unique and the average length was 1,744bp (Fig. 8). Preliminary comparisons involving *D. abbreviatus* + *C. maculatus* appear to reveal similar differentially expressed genes as to *D. ponderosae* + *S. oryzae*. Due to the great taxonomic distance between *D. ponderosae* and *S. oryzae*, not all reads of *D. ponderosae* successfully mapped onto the assembled transcriptome of *S. oryzae*. Those reads that did map, however, allowed for identification of differentially expressed transcripts (Fig. 10). The transcripts identified from the differential expression analyses were subsequently identified through Blast2GO® V.2.5.1, resulting in a list of 1,054 transcripts, and the distribution of GO terms plotted (Fig. 9). Of those transcripts, a reduced candidate gene list was produced of 57 genes which are hypothesized to be involved in rostrum development and differentiation (Table 1). This list was produced via assumptions of current knowledge of the respective genes and genetic pathways. As errors undoubtedly have been made in sorting through the original larger list of differentially expressed transcripts, the current list of 57 transcripts is considered tentative.

A comparison also was made between the transcriptomes derived from the prepupal and pupal heads of *S. oryzae,* in which a combined transcriptome of their respective transcripts was created to use as the mapping template during read mapping analyses with RSEM and Bowtie2. As a result of mapping the pupal and prepupal reads of *S. oryzae* onto their combined transcriptome, differential expression analyses resulted in a list of 1,410 transcripts (Fig. 11). Many of the transcripts found in the previous list were also found in this latter one, including several others, such as all five zinc finger domains of *broad complex* (including a putative sixth) and several *wnt* isoforms.

In *S. oryzae*, 32 of the 57 candidate genes (*Armadillo*, *Cap n collar, disco, distal-less*, *dorsal*, *engrailed*, *homothorax*, *Iroquois*, *pangolin, Juvenile hormone esterase*, *prospero, sex combs reduced*, *bric-a-brac2*, *broad complex z2*, *dachshund*, *decapentaplegic*, *discs large*, *Epidermal growth factor receptor*, *extradenticle*, *eyes absent*, *gasp*, *hairless*, *lethal giant larvae*, *Imaginal disc growth factor 2*, *LnK*, *nuclear hormone receptor hr3*, *orthodenticle 2*, *proboscipedia*, *singed, sonic hedgehog*, *split ends*, *wingless*) have been tested with RNAi and 5 (*armadillo*, *Cap n collar*, *homothorax*, *pangolin*, *sex combs reduced*) have been tested in *C. pardalis*. Of these 32 genes, 8 have shown significant changes in rostrum phenotype (*sex combs reduced, homothorax*, *distal-less*, *engrailed, split ends, bric-a-brac2, broad complex z2, nuclear hormone receptor hr3*), while the remainder currently are inconclusive due to high mortality.

In comparing some of these mutant phenotypes to the wild type (Figs. 12-19), *broad complex z2* RNAi perhaps causes the most dramatic phenotypic changes. Many of the diverse roles of the *broad complex* zinc finger array remains elusive, but it has been demonstrated that they are expressed at high levels just before and during metamorphosis and act to coordinate hormonally regulated growth of epidermal tissue (Konopova and Jindra 2008). In *S. oryzae*, knockdown of z2 is lethal (as it is in other insects) before reaching the adult, but in the pupa (Figs. 20-22) it dramatically reduces proliferation of the rostral tissue in comparison to the wild type (Fig. 27) and appears to allow partial reformation of the labrum (which is lost in all weevils excepting Nemonychidae and Anthribidae; Figs. 22-24).

*Distal-less* (*dll*) knockdown, while causing the expected distal shortening of appendages (e.g., Panganiban 2000), did not appear to have a major effect on rostrum formation (Figs. 28-30).

The effects of *engrailed* (*en*) RNAi was more pronounced in regions posterior to the head (Figs. 31-33). On the head, The median interocular fovea appears to have slightly enlarged. Perhaps most dramatic is the strange is the irregularly abbreviated pronotum and medio-longitudinal furrow which forms. As *en* patterns posterior compartments in each segment (e.g., Brower 1986), it is difficult at this time to explain the deformed pattern observed in the pronotum.

Similar to *dll*, the homeodomain-containing transcription factor *homothorax* (*htx*) is another genetic element upregulated during metamorphosis and is important in proper appendage development (e.g., Slattery *et al.* 2011). In *S. oryzae htx* RNAi (Figs. 34-37), among other malformations on the body and pronotum, the rostrum is markedly shorter, more robust, and curved.

*Split ends* (*spen*) is a transcription factor that interacts with antennapedia and Hox genes in the head, in which it promotes segment identity and sclerite development by also interacting with the EGFR pathway (e.g., Doroquez *et al.* 2007; Mace and Tugores 2004). RNAi of *spen* in *S. oryzae* results in a smaller individual, reducing the size of the head, compound eyes, and rostrum, as well as other features such as the elytra (Figs. 38-40).

The complex functions of *sex combs reduced* (*scr*) are still somewhat nebulous, partially due to its interactions with *antennapedia* and *fushi tarazu* (e.g., Calhoun and Levine 2003; Calhoun *et al.* 2002). It is a Hox gene in the Antennapedia complex and is also well-known for its suppression of dorsal appendages on the prothorax (wing rudiments) (e.g., Rogers *et al.* 1997). In *S. oryzae* RNAi (Figs. 41-50), this function in the prothorax is also visible. The resulting knockdown phenotype in the head and rostrum is quite interesting, in which the ventral surface of the head widens, caused by the reformation of the gula and subgenal sulci (Figs. 44-46, 48-49). At the rostral apex, the pleurostomal sulci also reappear (Figs. 47, 50).

## Discussion

Analyses of differential gene expression can be challenging among taxonomically disparate organisms due to wide evolutionary gaps between clades. Nonetheless, a number of genes have been identified as promising candidates. This study illustrates the utility of transcriptomics across wide phylogenetic distances to identify genes that may be responsible for key evolutionary innovations. It is intriguing that the comparison of *D. ponderosae* + *S. oryzae* had the highest portion of reads that reciprocally mapped, perhaps indicating that there is higher similarity among their sequences. This observation is most profound considering that many researchers support the phylogenetic hypothesis positing a derived position of bark beetles

(Scolytidae), one nested within the Curculionidae, as opposed to a position more basal to Dryophthoridae. Indeed, the greater similarity of *D. abbreviatus* + *C. maculatus* is of no surprise, as both taxa represent different subfamilies within Curculionidae; however, while it may be rather speculative to suggest, the greater similarity of *D. ponderosae* to *S. oryzae* than to either *D. abbreviatus* and *C. maculatus* may indicate greater phylogenetic separation of the bark beetles and the higher weevils.

Future work will entail continuing RNAi experiments for the remaining 24 candidate genes. Gene expression and RNAi data will then be compared to form hypotheses regarding the evolution of developmental pathways involved in rostrum formation. Examination of rostrum development, as with any morphological features, also will have remarkable influence in understanding homology statements when the relevant genetic elements involved in forming those structures are analyzed in comparison (e.g., Prud'homme *et al.* 2006).Together, these data will provide an extensive foundation from which to begin further research, including examination of these developmental genes in a broader phylogenetic context.

**Acknowledgements**

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**Table 1**. Filtered candidate gene list produced from differential expression analyses between *D. ponderosae* and *S. oryzae.*

| Seq. Description | Seq. Length | min. eValue | mean Similarity |
|---|---|---|---|
| **cuticular protein rr-2 family (agap001664-pa)** | 233 | 3.88E-06 | 65.85% |
| **cuticular protein rr-2 family (agap001664-pa)** | 523 | 1.73E-29 | 87.10% |
| **homeobox protein homothorax-like** | 805 | 9.54E-151 | 82.65% |
| **ubiquitin-conjugating enzyme e2r** | 2445 | 1.24E-140 | 87.10% |
| **sex combs reduced** | 1131 | 3.61E-84 | 94.85% |

| | | | |
|---|---|---|---|
| **partial** | 338 | 0.00344978 | 60.60% |
| **y box binding** | 1562 | 8.22E-53 | 89.65% |
| **broad-complex isoform z2** | 6430 | 0 | 61.90% |
| **tpa: cuticle protein** | 504 | 2.98E-30 | 62.00% |
| **broad-complex isoform z2** | 6438 | 0 | 62.30% |
| **protein singed-like** | 3633 | 0 | 85.00% |
| **gasp precursor** | 319 | 3.87E-75 | 86.40% |
| **staufen** | 3099 | 0 | 61.10% |
| **cuticular protein rr-2 family (agap001664-pa)** | 646 | 2.96E-28 | 87.40% |
| **protein hairless** | 2656 | 1.95E-72 | 65.45% |
| **probable nuclear hormone receptor hr3-like** | 4602 | 6.45E-140 | 88.75% |
| **risc-loading complex subunit tarbp2-like** | 1811 | 2.05E-162 | 68.95% |
| **chitin deacetylase-like isoform i** | 1699 | 7.01E-95 | 73.05% |
| **unknown [Dendroctonus ponderosae]** | 289 | 7.47E-25 | 89.00% |
| **unknown [Dendroctonus ponderosae]** | 307 | 1.54E-16 | 88.00% |
| **disco-interacting protein 2-like** | 5630 | 0 | 86.05% |
| **tpa: cuticle protein** | 2183 | 1.14E-40 | 46.70% |
| **rna binding protein fox-1 homolog 2-like** | 1011 | 9.36E-60 | 83.45% |
| **protein singed-like** | 424 | 1.59E-75 | 80.30% |
| **e3 ubiquitin-protein ligase iap-3-like** | 320 | 1.42E-28 | 65.85% |
| **pupal cuticle protein c1b (tm-c1b) (tm-pcp c1b)** | 630 | 6.31E-26 | 59.60% |
| **unkempt protein** | 2671 | 0 | 82.25% |
| **larval cuticle protein lcp-17-like** | 627 | 2.44E-25 | 62.95% |
| **endocuticle structural glycoprotein bd-8-like** | 577 | 1.47E-36 | 72.30% |
| **chitin deacetylase 2 isoform a precursor** | 425 | 3.35E-96 | 93.85% |
| **chitin synthase** | 2286 | 0 | 88.20% |
| **cuticle protein** | 366 | 4.36E-18 | 82.85% |
| **held out wings** | 1438 | 0 | 85.15% |
| **segmentation protein cap n collar** | 238 | 9.65E-39 | 94.35% |
| **unknown [Dendroctonus ponderosae]** | 386 | 2.59E-52 | 94.50% |
| **cuticular protein** | 851 | 9.30E-48 | 54.55% |
| **hormone receptor 4** | 3685 | 0 | 71.75% |
| **cuticle protein 8** | 400 | 6.40E-12 | 65.45% |
| **homeobox protein homothorax-like** | 1869 | 0 | 81.70% |
| **cuticular protein hypothetical 28 precursor** | 2328 | 0 | 52.60% |
| **protein hairless** | 2788 | 3.40E-72 | 65.45% |
| **epidermal growth factor receptor** | 1648 | 5.79E-61 | 51.95% |
| **cuticular protein** | 547 | 2.11E-06 | 66.25% |
| **imaginal disc growth factor 4** | 232 | 2.87E-38 | 70.50% |
| **cuticular protein rr-1 motif 48** | 1076 | 4.89E-76 | 57.05% |
| **larval cuticle protein a3a** | 333 | 1.74E-40 | 75.90% |

| | | | |
|---|---|---|---|
| **homeobox protein prospero prox-1** | 2063 | 0 | 72.10% |
| **dorsal** | 243 | 8.10E-22 | 72.30% |
| **tpa: cuticle protein** | 1080 | 3.33E-47 | 85.85% |
| **adult cuticular protein** | 409 | 2.95E-24 | 66.95% |
| **iroquois-like protein** | 1322 | 2.20E-165 | 88.70% |
| **cuticle protein** | 603 | 1.29E-33 | 91.90% |
| **epidermal growth factor receptor** | 3838 | 0 | 76.70% |
| **armadillo segment polarity** | 243 | 1.01E-19 | 81.65% |
| **basic helix-loop-helix protein** | 1197 | 1.02E-40 | 74.05% |
| **pangolin** | 734 | 1.60E-51 | 72.25% |

## Figure legends

**Fig. 1**. A perusal of rostral diversity within the weevil superfamily Curculionoidea.

**Figs. 2-7**. 2-6, Taxa for which transcriptomes were obtained. 2, *Callosobruchus maculatus* (Chrysomelidae: Bruchinae); 3, *Dendroctonus ponderosae* (Scolytidae); 4, *Sitophilus oryzae* (Dryophthoridae); 5, *Curculio pardalis* (Curculionidae: Curculioninae); 6, *Diaprepes abbreviatus* (Curculionidae: Entiminae). 7, flowchart showing general workflow of this study.

**Figs. 8-9**. 8, Contig lengths of resulting de-novo transcriptome assembly using Trinity. 9, Distribution of gene ontology (GO) terms among differentially expressed transcripts of comparison between prepupae of *S. oryzae* and *D. ponderosae*.

**Figs. 10-11**. Fold-change plots generated by EdgeR. 10, Comparison between prepupae of *S. oryzae* and *D. ponderosae*; blue threshold line indicating fold-change of 4. 11, Comparison between pupa and prepupa of *S. oryzae*; blue threshold line indicating fold-change of 2.

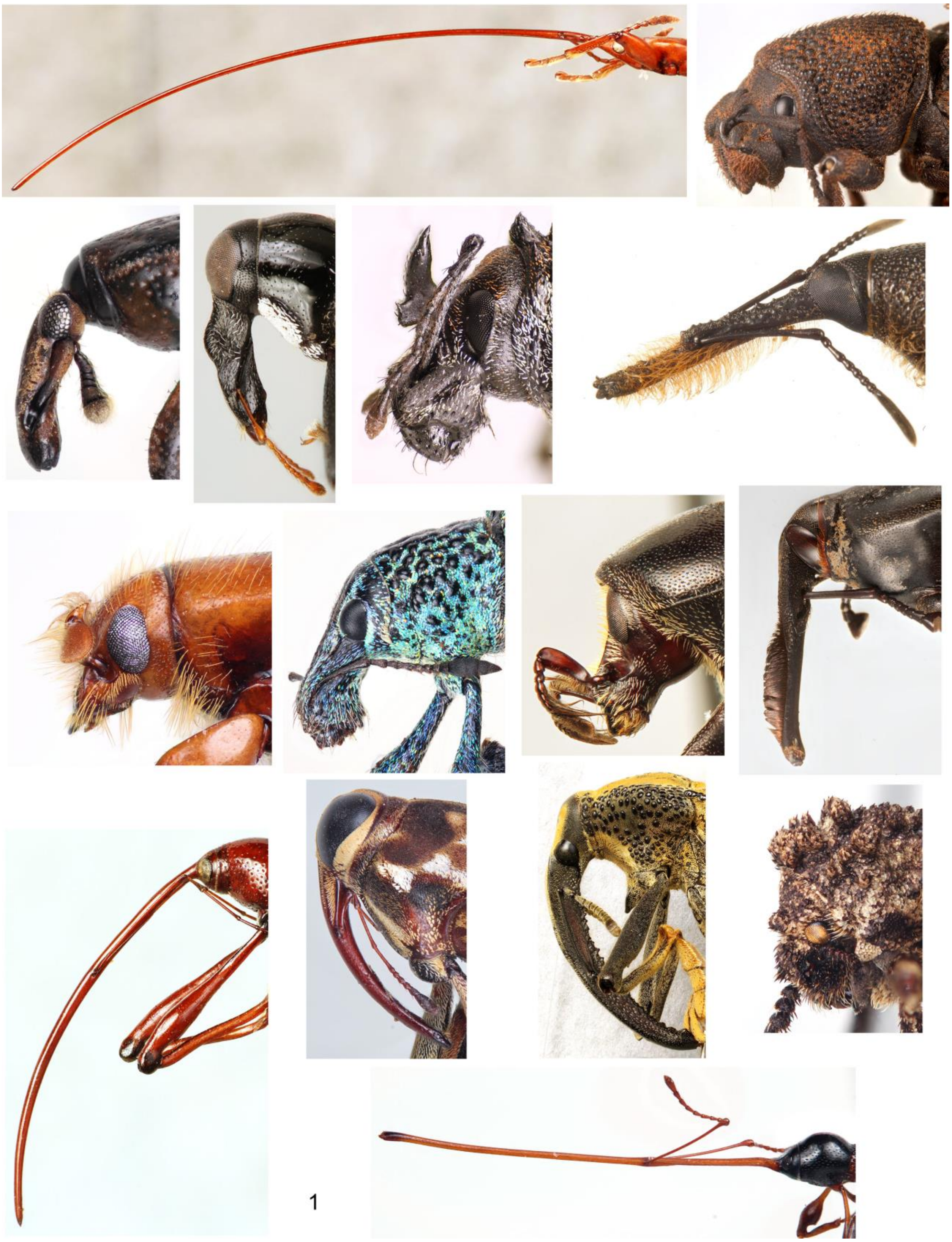
**Figs. 12-19**. Wild type of *S. oryzae*. 12-15, photomicrographs. 12, male, dorsal aspect; 13, male, lateral aspect; 14, female, dorsal aspect; 15, female, lateral aspect. 16-19, SEM's of head. 16, anterior aspect; 17, dorsal aspect; 18, lateral aspect; 19, ventral aspect.

**Figs. 20-27**. 20-24, 25-26, Mutant phenotype resulting from *broad complex z2* RNAi. 20-22, photomicrographs. 20, adult, dorsal aspect; 21, adult, lateral aspect; 22, head, anterior aspect, showing labrum. 23, SEM of head, anterior aspect; 24, enlargement of rostral area of 23, showing labrum. 25-27, semi-thin longitudinal sections of head. 25, head, showing labrum; 26, enlargement of anterior portion of head, showing distinct labrum, hinge area of labrum, and reduced presence of rostral tissue; 27, wild type, prepupal head.

**Figs. 28-33**. 28-30, Mutant phenotype of adult resulting from *dll* RNAi. 28, dorsal aspect; 29, lateral aspect; 30, antero-dorsal aspect of head. 31-33, Mutant phenotype of adult resulting from *en* RNAi. 31, dorsal aspect; 32, lateral aspect; 33, antero-dorsal aspect of head.

**Figs. 34-40**. 34-37, Mutant phenotype of adult resulting from *htx* RNAi. 34, dorsal aspect; 35, lateral aspect; 36, anterior aspect of head; 37, lateral aspect of head. 38-40, Mutant phenotype of adult resulting from *spen* RNAi. 38, dorsal aspect; 39, lateral aspect; 40, antero-dorsal aspect of head.

**Figs. 41-50**. Mutant phenotype of adult resulting from *scr* RNAi. 41-44, photomicrographs. 41, dorsal aspect; 42, lateral aspect; 43, anterior aspect of head; 44, ventral aspect of head, showing widely-separated occipital sulci and presence of a gula (signified by the brief postoccipital sulci). 45-47, SEM's of ventral side of head. 45, head, ventral aspect, showing widely-separated occipital sulci and presence of a gula; 46, enlargement of gular area of 45; 47, enlargement of apical area of rostrum of 45, showing presence of the pleurostomal sulci. 48-50, semi-thin cross sections of the head. 48, section at middle of rostrum, showing presence of both occipital and subgenal sulci, as well as their respective apodemes; 49, section at beginning of the head (base of rostrum), showing presence of the posterior tentorial arms; 50, section at apex of rostrum, showing presence of the pleurostomal sulci.



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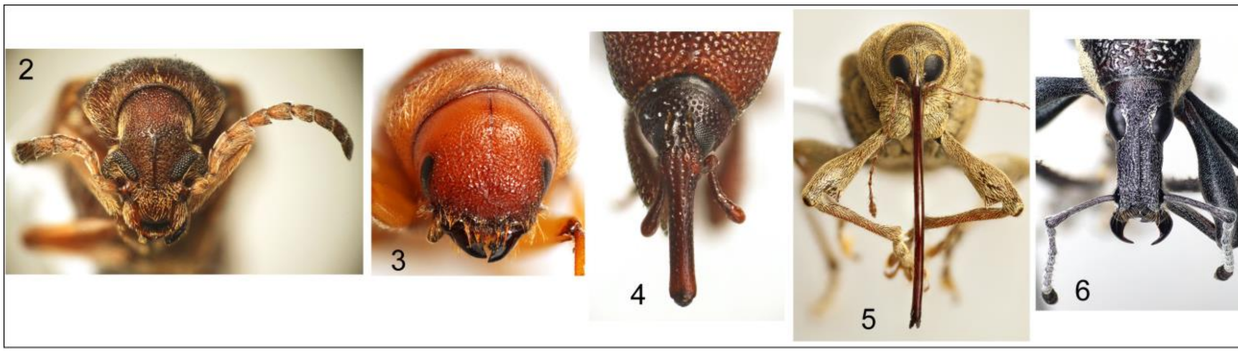
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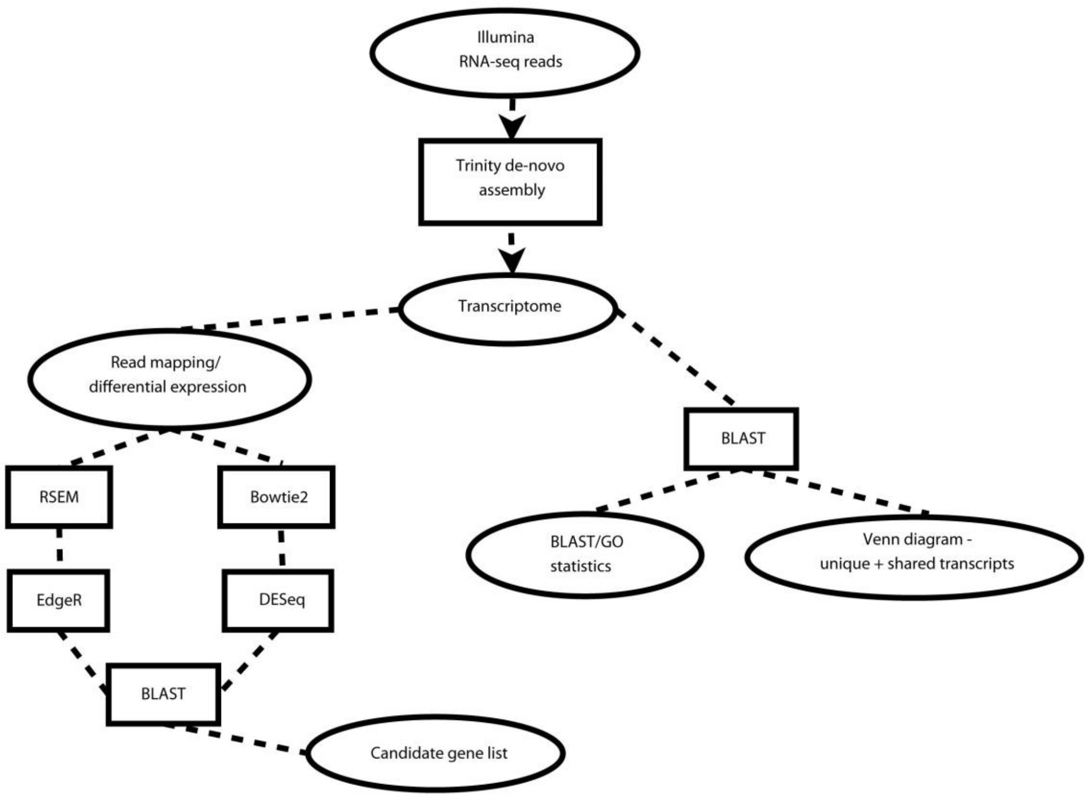
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Read mapping/
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BLAST/GO
statistics
Venn diagram -
unique + shared transcripts

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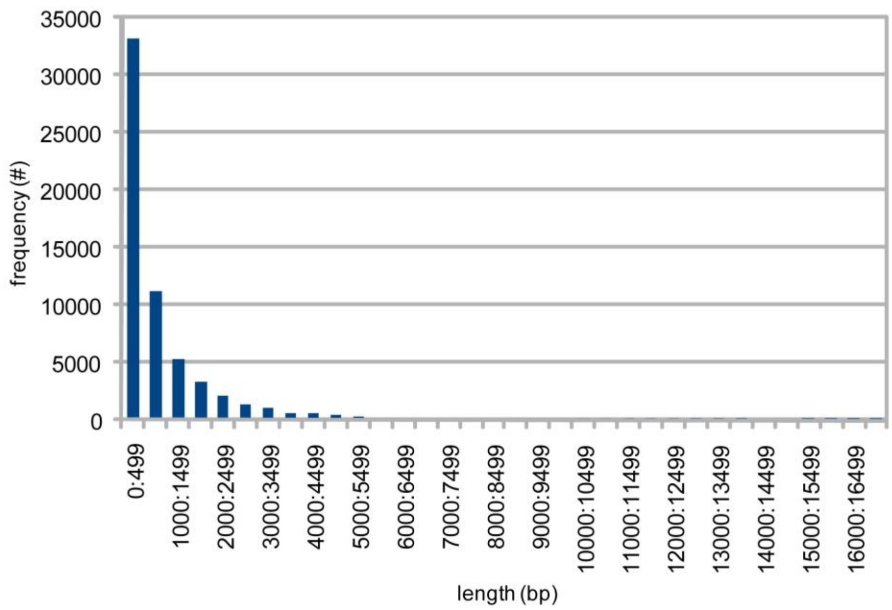
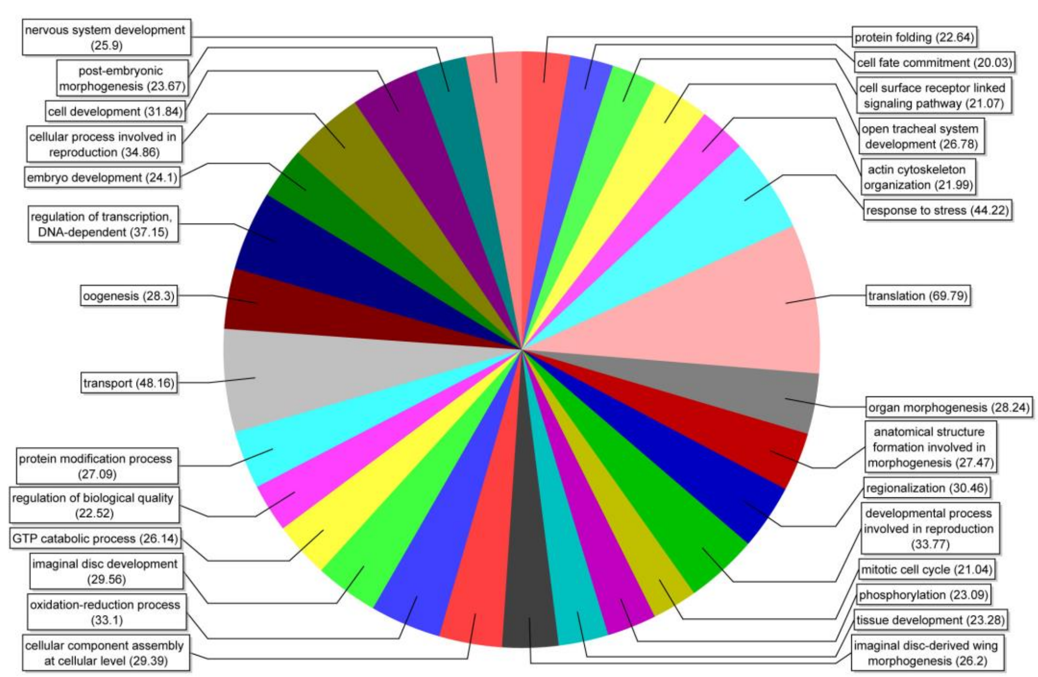
Figure 8. Contig lengths (*Sitophilus oryzae*)



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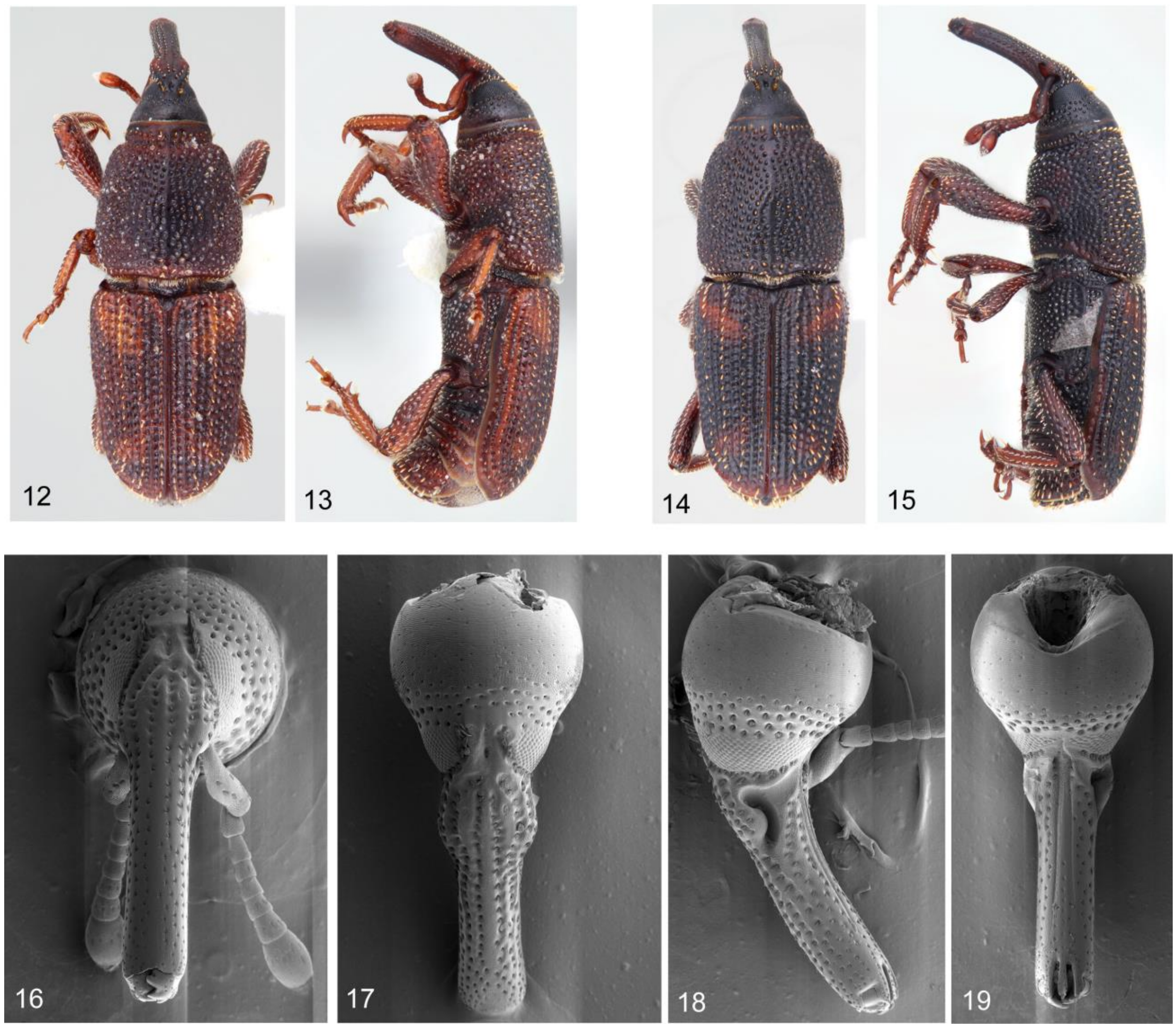
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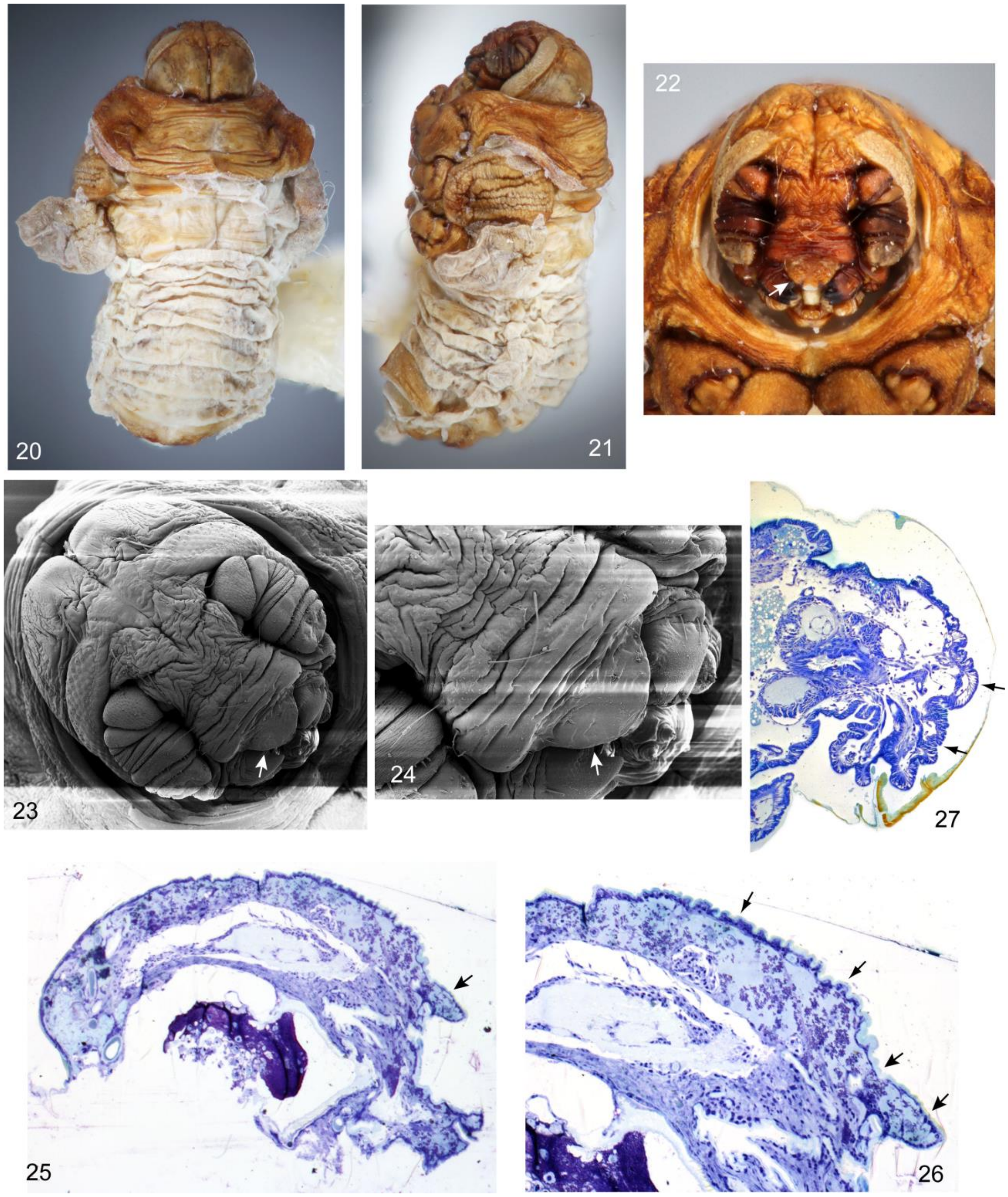
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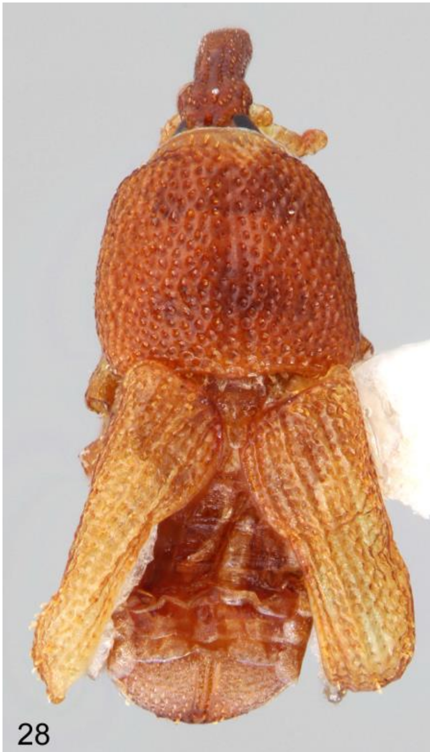
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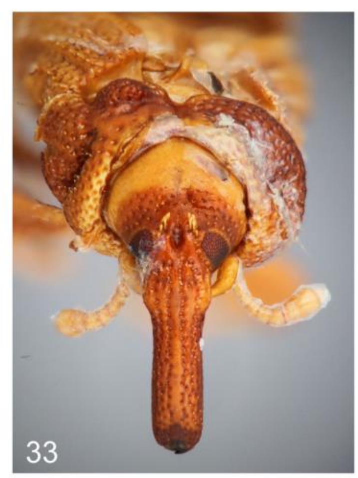
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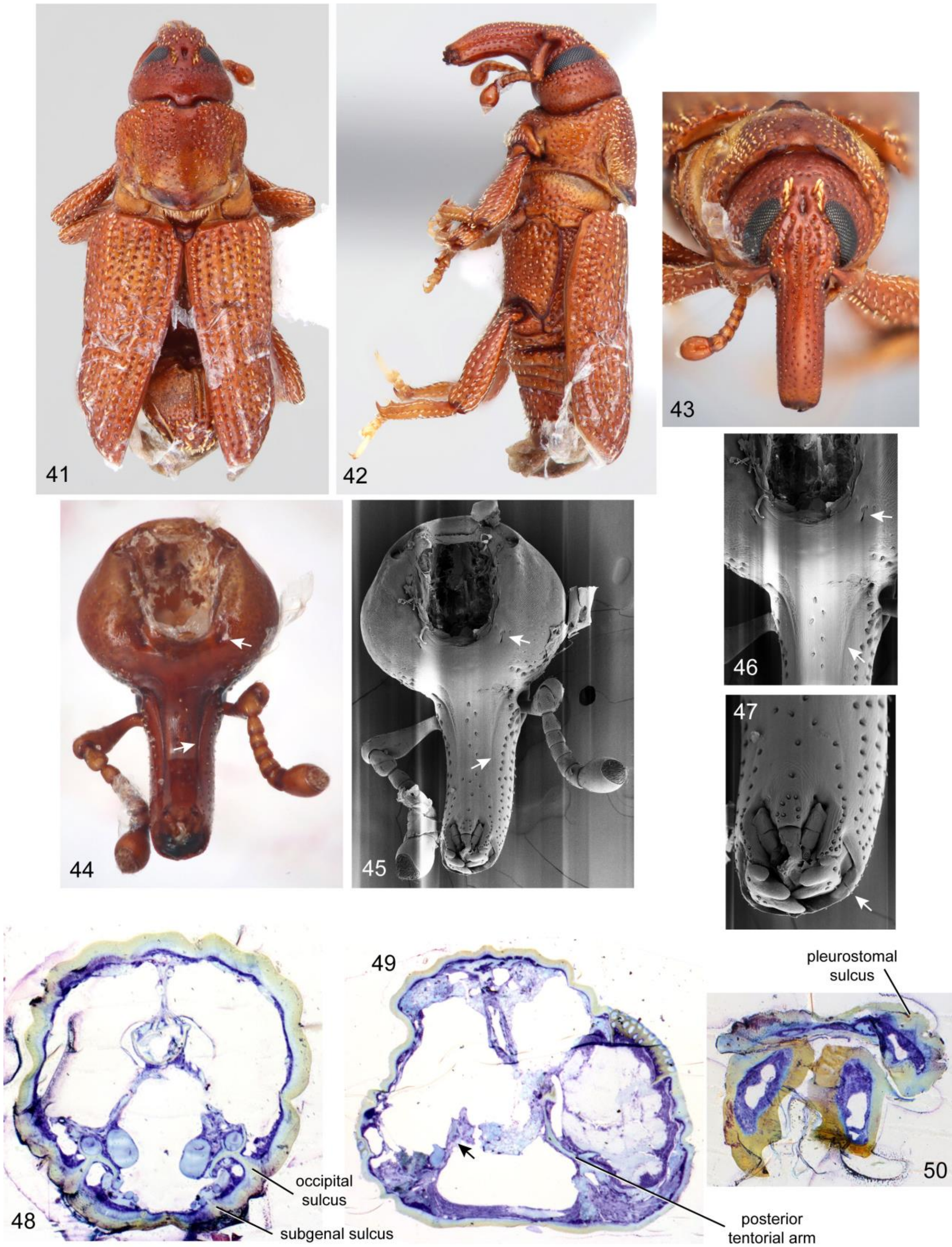
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pleurostomal sulcus
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subgenal sulcus
posterior tentorial arm

# 7. A comparative review of beetle cuticles, with an emphasis on the structure of weevil cuticles (Coleoptera: Curculionoidea)

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## Abstract

Significant progress has been made in the study of insect integument and determining the cuticular structures found in several different insect groups. Relatively recently, much attention has been paid to beetle cuticle, particularly in characterizing the structure of elytra due to their rigid construction. While beetles are noted for their stiff cuticles, weevils have a notably stronger cuticle that is apparent simply when attempting to pin a collected specimen. A more extensive study, therefore, has been attempted to further characterize the cuticle of weevils and to compare it to that of other Coleoptera to formulate a basic understanding of its composition and provide a basis for further avenues of research. Thin sections were made of the elytra, rostrum, and in a few cases the pronotum and compound eye, in exemplar weevil taxa throughout Curculionoidea. These sections reveal differences in cuticular thickness and composition in comparison to other coleopterans, as well as to other families within the superfamily. A distinct procuticular layer between the endo- and exocuticle, possibly representing a mesocuticle, is also present and characterized in several weevil taxa.

## Introduction

The general structure of the insect cuticle has been studied and reviewed by numerous authors, including Filshie (1970), Fraenkel and Rudall (1947), Kramer *et al.* (1988), and Wigglesworth (1948a, b). The generalized insect integument begins with the living basement membrane and epidermal cells, followed by the non-living cuticular portion consisting of the procuticle (divided into an endocuticle and exocuticle) and epicuticle. An intermediate layer between the endocuticle and exocuticle, the mesocuticle, has been identified in some insects and is characterized as an untanned region like the endocuticle, but with similar proteins and lipids as the exocuticle. The epicuticle does not contain chitin and can be subdivided into several layers containing various lipids, lipoproteins, and hydrocarbons. The procuticle mostly is composed of several different types of proteins (earlier categorized under the single name arthropodin, but now several hundred different proteins have been identified), chitin, and in particular areas, resilin.

Generally. the endocuticle is colorless and is the thickest component of the cuticle, and the exocuticle is often gold to reddish-brown and typically composes about 1/3 of the thickness of the cuticle (Wigglesworth 1948b). In beetles, these ratios tend to be quite different, in which the exocuticle composses much less of the thickness in comparison to the endocuticle (Krzelj 1969; Van de Kamp and Greven 2010). Although the exocuticle is often referred to as the strengthening component of the cuticle (as it certainly is recognized as being the hardest part of the cuticle [Müller *et al.* 2008]) and the endocuticle as the more flexible component that is dominant in the cuticle of soft-bodied insects, the thickening of the endocuticle in Coloeoptera is thought to provide greater rigidity. While many fairly recent studies have focused on determining the structure and mechanical properties of beetle cuticle (Chen *et al.* 2000, 2001, 2002, 2004, 2006, 2007; Chen and Ni 2003; Dai and Yang 2010; Hepburn and Ball 1973; Krzelj 1969; Leschen and Cutler 1994; Müller *et al.* 2008; Van de Kamp and Greven 2010; Yang and Dai 2008; Yang *et al.* 2010), particularly due to the hardness of their elytra as compared to other insect cuticles, few studies have incorporated exemplars of weevils (Curculionoidea). Indeed, the cuticle found in Coleoptera is quite firm and stiff, but the cuticle of many weevil groups, such as those in the crown family Curculionidae, often are composed of many more layers of endocuticle and are significantly more stiff. While weevil cuticle is generally considered here to be more rigid relative to most other beetle cuticles, this hardness is referenced here as a qualitative feature, as it has yet to be assessed quantitatively. Therefore, a comparative review of the generalized cuticle of beetles, with an emphasis on some of the harder cuticles found across the curculionoid clade, is of most interest. Although the cuticle of weevils is generally recognized as being stronger and more rigid than most other beetles, the reason for this robustness is understudied and requires further examination.

## Materials and Methods

### *Taxon sampling*

Of the recognized 19 extant families in Curculionoidea (*sensu* Alonso-Zarazaga and Lyal 1999), 8 are sampled in this study (Table 1). In the most diverse family, Curculionidae, with 16 recognized subfamilies, 8 are sampled in this study. Sampling strategy focused on examining a few regions of cuticle on the weevil body in a diverse range of exemplar taxa.

**Table 1**. Weevil (Curculionoidea) taxa sampled (classification following Alonso-Zarazaga and Lyal 1999); sections of the body: E=elytron, R=rostrum, P=pronotum, CP = compound eye.

| **Family** | **Subfamily** | **Species** | **E** | **R** | **P** | **CP** |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| Anthribidae | Anthribinae | *Euparius paganus* | X | X | | |
| Attelabidae | Apoderinae | *Cycnotrachelus* (*Cychnotrachelodes*) *roelofsi* | | X | | |
| Rhynchitidae | Rhynchitinae | *Rhynchites* spp. | | X | | |
| Brentidae | Brentinae | *Arrhenodes minutus* | X | X | | X |
| Scolytidae | | *Xyleborus* spp. | X | | | |
| Platypodidae | | *Platypus* spp. | | X | | |
| Dryophthoridae | Rhynchophorinae | *Rhodobaenus* spp. | X | | | X |
| Dryophthoridae | Rhynchophorinae | *Sitophilus oryzae* | X | | | |
| Dryophthoridae | Rhynchophorinae | *Sphenophorus* spp. | X | | X | |
| Curculionidae | Ceutorhynchinae | *Auleutes* spp. | X | | | |
| Curculionidae | Curculioninae | *Smicronyx squalidus* | X | | X | |
| Curculionidae | Cryptorhynchinae | *Chalcodermus collaris* | X | | | |
| Curculionidae | Cryptorhynchinae | *Tyloderma variegatum* | X | | X | |
| Curculionidae | Entiminae | *Cyrtepistomus castaneus* | X | | | |
| Curculionidae | Entiminae | *Epicaerus imbricatus* | X | | | |
| Curculionidae | Hyperinae | *Hypera eximia* | | X | | |
| Curculionidae | Lixinae | *Lixus* spp. | | X | | |
| Curculionidae | Molytinae | *Conotrachelus* spp. | X | | | |
| Curculionidae | Molytinae | *Rhyssomatus lineaticollis* | X | | | |
| Curculionidae | Baridinae | *Odontocorynus* spp. | | X | | |

*Histological sections + general microscopy*

Adults used for histological examinations were sometimes fresh or were otherwise stored in 95% alcohol. The appropriate parts (elytra, prothorax, etc.) were disarticulated from the body and transferred to paraformaldehyde for ~1 day. The head + prothorax were then transferred to LR White (Electron Microscopy Sciences) for ~1 day. For embedding, body parts were placed in gelatin capsules filled to the top with LR White and then in an oven for ~24 hours at 60°C (thermal curing). After polymerizing, embedded specimens were removed from the capsules and sectioned using a Leica EM UC6 ultratome and diamond knife, producing thin sections ~5000–6000 nm thick. Sections were transferred to glass slides by heating them on a slide warmer for ~30 minutes followed by staining in toluidine blue. Stained sections were digitally photographed with a Canon EOS-1 camera mounted on an Olympus BX51 compound microscope. Regarding most photomicrographs, a z-stack was acquired of several images, combined using the software CombineZ, and edited in Adobe Photoshop CS3.

*Electron microscopy*

Scanning Electron Microscope (SEM) images were captured using a LEO 1550 FESEM (Field Emission Scanning Electron Microscope). Specimens and dissections were mounted on SEM stubs using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite, and coating was performed using gold.

## Results

After surveying various exemplar taxa from across Curculionoidea, the general structure of the cuticle (Fig. 1) follows that reported by Van de Kamp and Greven (2010), in which the procuticle is composed of balkens, unidirectional bundles of chitin (referred to as macrofibrils by Leopold *et al.* 1992). This balken type of cuticle deposition is superficially different from the laminate type due to the separate, visible chitin macrofibers (Figs. 2, 3). The mechanism by which these separate fibers are formed is unknown; however, it has been reported that they arise as parallel thickenings or bundles from the underlying lamina (Richards 1951). This structure is also similar to that of the elytra of most coleopteran families, such as Chrysomelidae, Tenebrionidae, and Cerambycidae (Krzelj 1969). While most Coleoptera seem to possess the balken-type of procuticle, there are a few families that possess the plywood-/lamellar-type (Van de Kamp and Greven 2010). All of the exemplar taxa examined in this study possess the balken-type of procuticle, suggesting that possibly most weevils share this form. Van de Kamp and

Greven (2010), however, reported that *Otiorhynchus ovatus* possesses both balken and lamellar types of procuticle, in which the basal layers are arranged as lamellar sheets, transferring to balkens at the upper layers.

Also, in general, it appears that thicker procuticles (with up to 25 balken layers) are found mostly in the higher weevils (Curculionidae), possessing numerous balken layers in the endocuticle that are successively layered in ~30°-90° rotations (Fig. 4). The exocuticle also varies in thickness, generally thicker in taxa that also possess a relatively thick endocuticle (Figs. 5, 13, 21, 23-28, 39); however, this trend is quite variable, particularly when examining the cuticle in other regions of the body, such as the rostrum and pronotum. Occasionally, a thin exocuticle accompanies a rather thick endocuticle (Figs. 8, 11, 16-18, 20, 22); the opposite is somewhat less common, in which a relatively thick exocuticle accompanies a thin endocuticle (Fig. 37). Along with variation in cuticle thickness, there is variability seen in the size of the hemolymph space in the elytra. Taxa that possess fairly thick elytral cuticle often also have relatively small hemolymph spaces (Figs. 6-8, 19); taxa with fairly thin cuticle usually also possess larger hemolymph spaces (Figs. 14, 15, 34-36), and of course there are taxa that possess somewhat intermediate stages of cuticle thickness and hemolymph space (Figs. 9, 10, 16, 17). These correlations are not always observable, but they appear to be moderately constant. What also is rather curious is the presence of a darker-stained region, typically between the endo- and exocuticle in many taxa (Figs. 5, 7, 14, 15, 23, 28, 31-33, 40), but also found between layers of endocuticle (Fig. 33), similar to a pattern observed by Müller *et al.* (2008) in *Pachnoda marginata* (Coleoptera: Scarabaeidae). Although this region resembles the endocuticle in structure, it may have a different composition of proteins and could possibly represent what has been noted in some insects as a mesocuticle (Lower 1957). Despite its similarity to the endocuticle, it appears to be slightly denser, as indicated by its darker staining, and largely composed of tall, parallel fibers (Figs. 28, 32).

The compound eyes were also sectioned to examine relative thicknesses of the endocuticle and exocuticle, mostly due to a reiteration in the literature of a synapomorphy for Brentidae, namely the eye being covered by a corneal lens (Oberprieler et al. 2007). Although this character description seems faulty, as all weevil ommatidia certainly have corneal lenses, there are some notable differences. In this study it is apparent that the corneal lenses in Brentidae are quite thick (Fig. 41). Their actual synapomorphy is not the presence of a corneal lens but is the apparent fusion of the lenses to form a smooth, contiguous surface, in which the lenses are not differentiable as discrete units. The endocuticle composes most of the thickness of the lens, while the exocuticle is very thin. In comparison, in the dryophthorid taxon sampled (*Rhodobaenus* spp.; Fig. 31), the corneal lenses are discrete units and are quite thin, in which the endocuticle is reduced in thickness while the exocuticle remains similar in thickness to that in Brentidae. In Anthribidae (Fig. 38) the lenses are thicker than those in Dryophthoridae and appear most similar in structure to them as well; however, the thickness of the endocuticle appears more similar to that in Brentidae. The characterization of the corneal lens in weevils, therefore, seems to be one of confusion and requires further examination.

## Discussion

While the basic structure of weevil cuticle is similar to that of Coleoptera and Insecta, it is apparent that the comparatively thinner procuticle of basal weevil groups (e.g. Nemonychidae, Anthribidae, Rhynchitidae, Attelabidae, Brentidae) to the crown groups (e.g. Dryophthoridae, Brachyceridae, Curculionidae) as well as to various other Coleoptera, contributes to their weaker strength. Furthermore, the greatly thickened and robust procuticle of the crown weevil groups may be the primary reason for their particular hardness; however, given the great diversity of proteins that have been found in the procuticle (Missios *et al.* 2000), it would not be surprising that differences in protein composition may also significantly contribute to the unusual strength of weevil cuticle. The presence of a distinguishable cuticular layer between the endo- and exocuticle, tentatively identified here as a mesocuticle, may also contribute to the overall greater rigidity of the cuticle. Although there is this possibility, the presence of a mesocuticular layer in various groups seems to complicate the examination of any patterns. From the examined taxa, a distinct mesocuticle often is present in thick cuticles (Figs. 5-7, 23, 28, 31), although it is also found in thinner cuticles (Figs. 14, 15, 32, 33, 40).

In addition to the factors mentioned above, the general presence of a balken-type procuticle in weevils may also provide a greater rigidity over the lamellar-type of procuticle, though this hypothesis has not been studied empirically. The latter type is analogous to plywood (a sturdy construction of its own), which is heterogeneous in composition. The former type is homogeneous and uniform in composition, analogous to parallel sets of iron bars that reinforce concrete structures. Even though a clear distinction is made between these two types of procuticle, there likely exists a continuum of cuticle types, in which these two represent divergent forms, as many times the difference between balken- and ply-types is ambiguous and the balkens consist of wide, anastomosing macrofibrils that resemble a lamellar sheet. Although the formation of this balken-type remains unclear, it is hypothesized that the orientation of at least the first basal layer is in direct control of the epidermal cells (Leopold *et al.* 1992). The mode by which successive layers are then deposited at different angles, though, probably is under less direct control of the epidermis and may be due to more physical factors. It is also interesting to note that the balken-type of procuticle is deposited more quickly that the lamellar-type, another mechanism left unresolved.

The balken layers of the procuticle, although typically appearing to be successively layered at approximately 30-45° angles, usually differ in the angles at which they are layered. These layers may possess fibers that are positioned at 30°, 60°, or 90° angles, or at angles in between. Some cuticles may possess layers angled at fairly regular intervals, and others may have a mixture of angles (Leopold *et al.* 1992). The angle between lamellar or balken layers may also vary in different body regions, possibly suggesting that regional cuticles are adapted to handle specific mechanical stresses. As already mentioned, the number of layers varies from being rather few (~5) to being quite numerous (~25). This vast variation in the number of procuticular layers is seen in cuticles ranging from the rostrum, the pronotum, and to the elytra. Although it is difficult to formulate a pattern to explain differences in cuticular thickness in the thorax, abdomen, and elytra, a weak, but logical, pattern does appear to emerge in cuticular thickness of the rostrum. Generally in taxa with a short rostrum (such as in Entiminae), which typically are not drilling deep holes in plant tissue (e.g. Anthribidae), the rostrum is composed of a cuticle with relatively few layers of procuticle (Fig. 37). The majority of weevil groups, however, feed and oviposit in various plant tissues; their rostra must be more rigid to support these behaviors, thus they usually have a greater thickness of the procuticle (Figs. 26-30, 32, 33, 39, 40).

While it is not always the case, cuticular thickness in the elytron appears to correlate fairly strongly with the volume of hemolymph space present. This correlation was briefly discussed by Van de Kamp and Greven (2010), in which they postulated that thinner cuticles tend to be in taxa that are active flyers. To reduce body mass and permit improved flying capability, these taxa generally also possess large hemolymph spaces in the elytra. Conversely, taxa that are apterous, brachypterous, or are capable of flying but only do so rarely, usually have a small volume of hemolymph space and thicker cuticle, as they can afford to utilize greater resources for these structures.

Regarding reasons for why such rigid cuticle is found in the higher weevils remain little discussed and unknown. It seems that groups found in arid habitats tend to have tougher cuticles, possibly to help reduce water-loss; however, rigid cuticles are also found in tropical and temperate weevil groups. This phenomenon leaves much uncertainty and much room for further study.

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**Figure captions**:

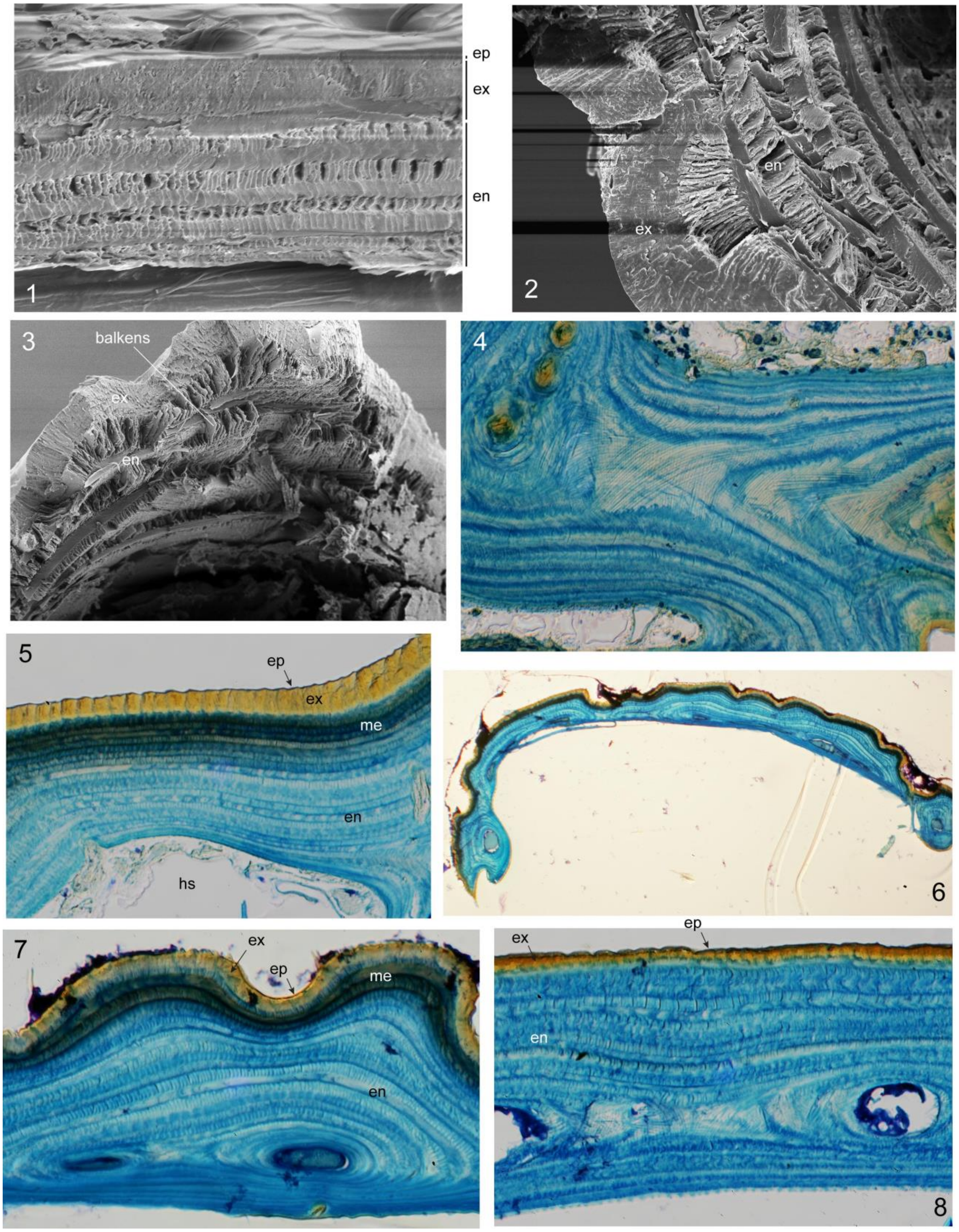
**Figs. 1-8**. 1-3, SEM micrographs of rostrum cuticle of *Sitophilus oryzae*. 1, longitudinal section exposing layers of rostrum cuticle; 2-3, cross sections exposing layers and balkens of rostrum cuticle. 4-8, thin cross sections of weevil elytron cuticle. 4-5, *Rhyssomatus lineaticollis*; 6-7, *Sphenophorus* spp.; 8, *Chalcodermus collaris*. ep = epicuticle, ex = exocuticle, me = mesocuticle, en = endocuticle, hs = hemolymph space of elytron.

**Figs. 9-15**. Thin cross sections of weevil elytron cuticle. 9-10, *Xyleborus* spp.; 11, *Auleutes* spp.; 12, *Arrhenodes minutus*; 13, *Smicronyx squalidus*; 14-15, *Cyrtepistomus castaneus*. ep = epicuticle, ex = exocuticle, me = mesocuticle, en = endocuticle, epid = epidermal cells, hs = hemolymph space of elytron, tr = trachea.

**Figs. 16-23**. 16-22, thin cross sections of weevil elytron cuticle. 16-18, *Epicaerus imbricatus*; 19-22, *Tyloderma variegatum*. 23, *Sphenophorus* spp., thin cross section of pronotum. ep = epicuticle, ex = exocuticle, me = mesocuticle, en = endocuticle, epid = epidermal cells, hs = hemolymph space of elytron, tr = trachea.

**Figs. 24-31**. Thin cross sections of weevil cuticle. 24-25, cuticle of pronota. 24, *Tyloderma variegatum*; 25, *Smicronyx squalidus*. 26-30, cuticle of rostra. 26-27, *Lixus* spp.; 28, *Rhodobaenus* spp.; 29, *Hypera eximia*; 30, *Arrhenodes minutus*; 31, *Rhodobaenus* spp., junction at head and compound eye, partially showing ommatidia and relatively thin endocuticle of corneal lenses; arrows pointing to exocuticle of corneal lenses. ep = epicuticle, ex = exocuticle, me = mesocuticle, en = endocuticle, epid = epidermal cells.

**Figs. 32-41**. Thin cross sections of weevil cuticle. 32-33, cuticle of rostra. 32, *Rhynchites* spp.; 33, *Platypus* spp. 34-38, *Euparius paganus*. 34-36, cuticle of elytra; 37, cuticle of rostrum; 38, cuticle of compound eye, partially showing ommatidia and the thickened endocuticle of corneal lenses; arrows pointing to exocuticle of corneal lenses. 39-40, cuticle of rostra. 39, *Odontocorynus* spp.; 40, *Cycnotrachelus* (*Cychnotrachelodes*) *roelofsi*. 41, *Arrhenodes minutus*, cuticle of compound eye, partially showing ommatidia and the thickened endocuticle of corneal lenses; arrow pointing to fused, uniform exocuticle of corneal lenses. ep = epicuticle, ex = exocuticle, me = mesocuticle, en = endocuticle, epid = epidermal cells, hs = hemolymph space of elytron.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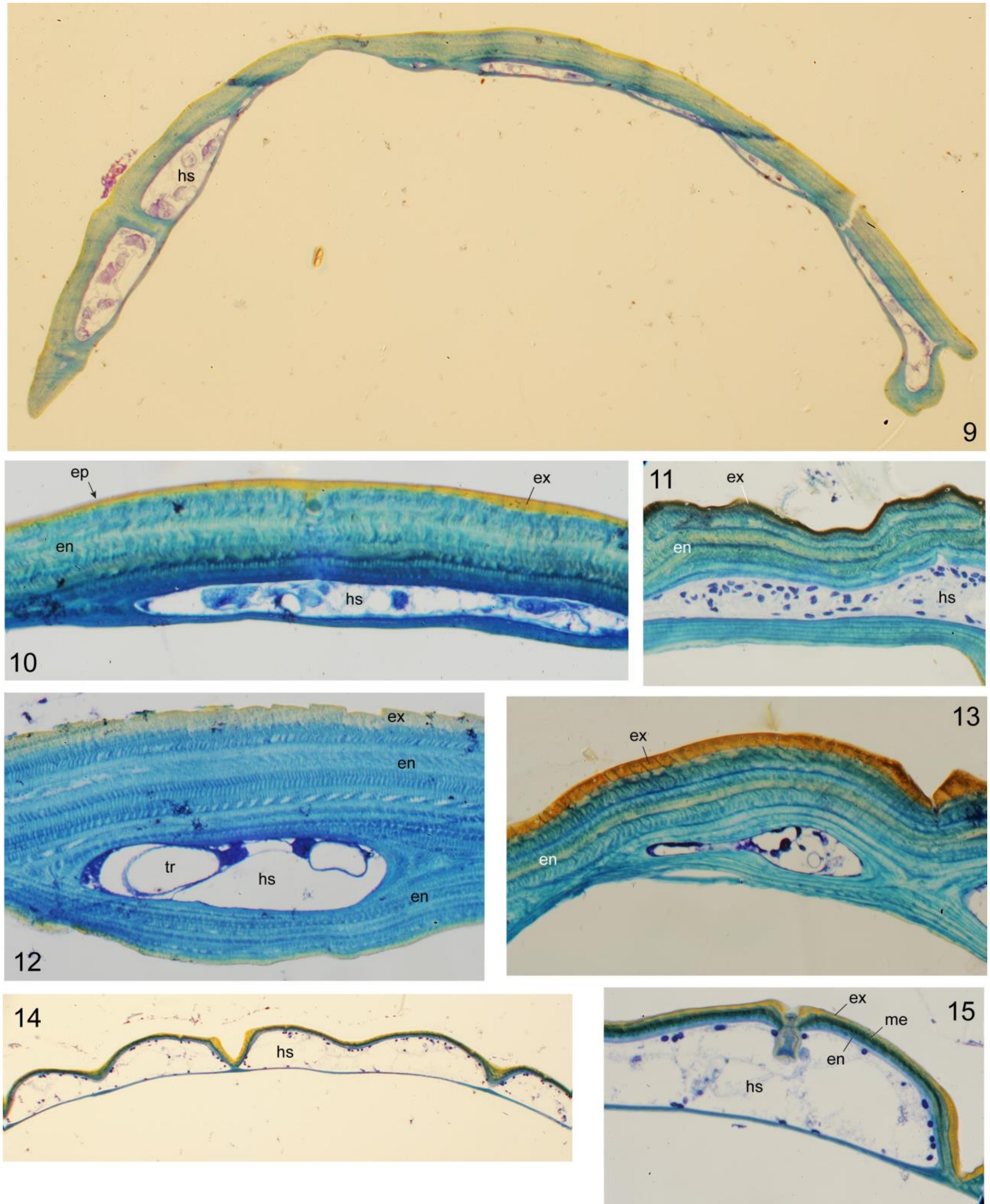
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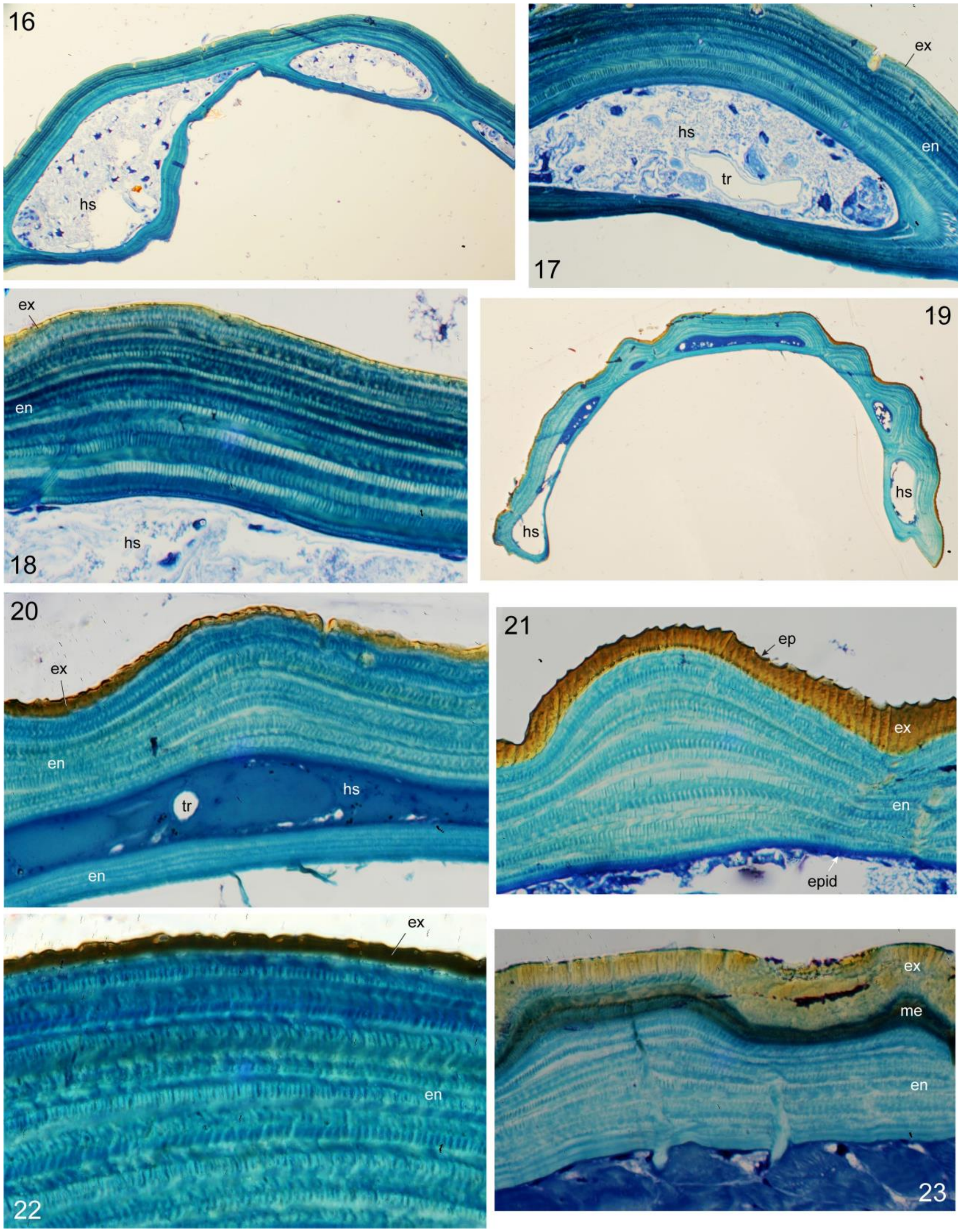
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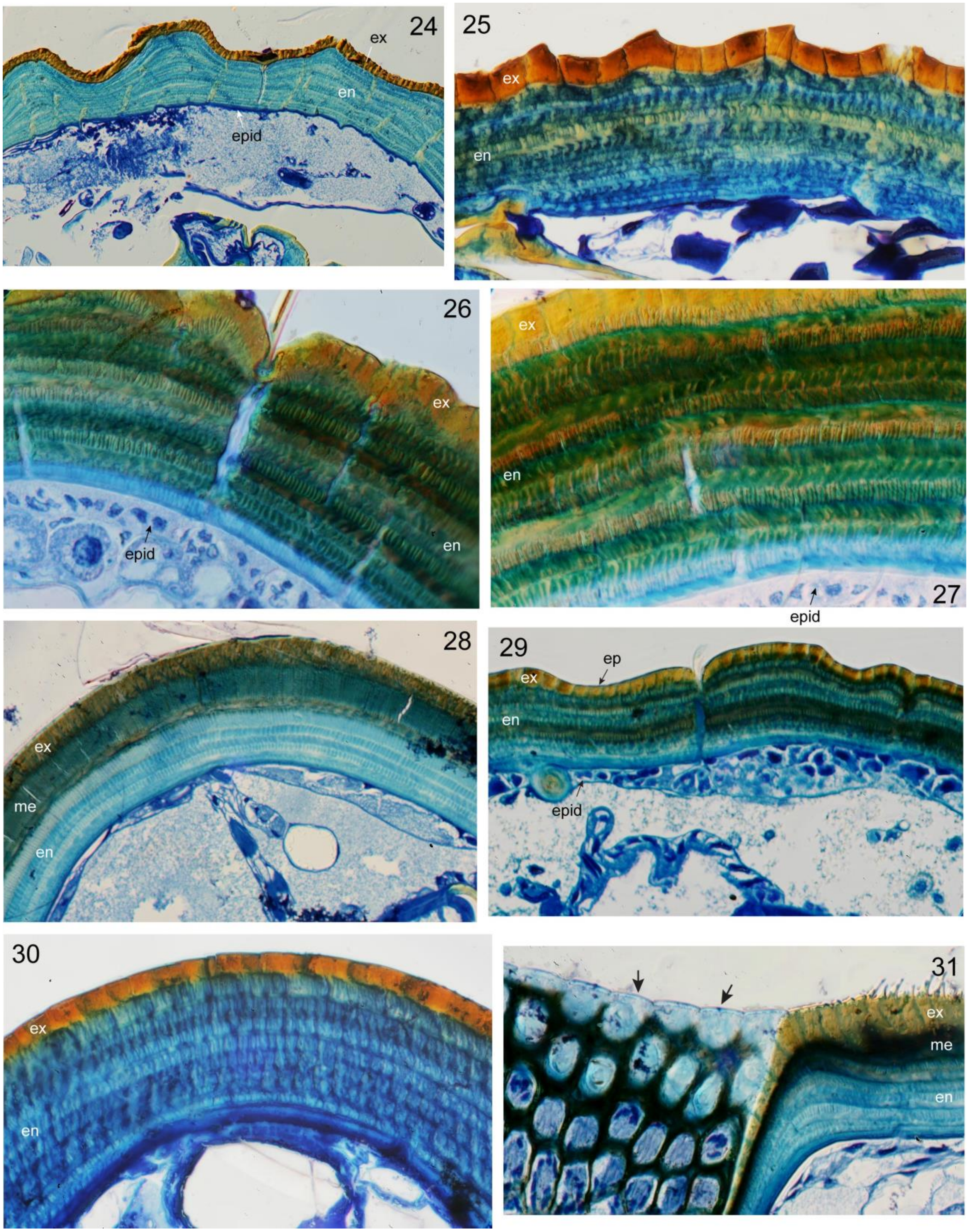
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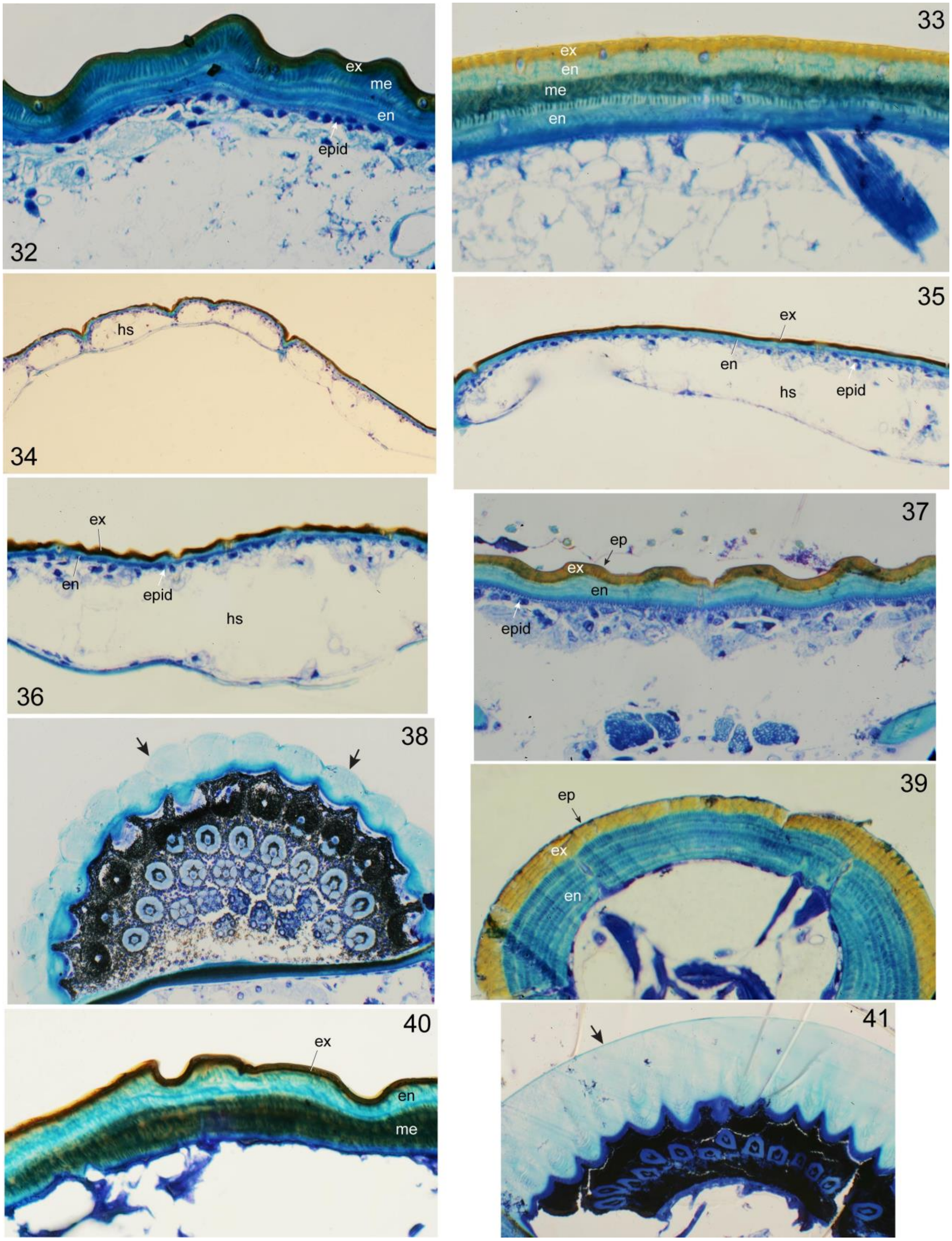
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## 8. Conclusions and future directions

Beetles (Coleoptera) are a fantastic radiation of insects, containing more than 350,000 extant species. Weevils (Curculionoidea) are one of the largest radiations within Coleoptera, the extant fauna alone comprising more than 25% of Polyphaga, one of the four suborders of beetles itself occupying 90% of the diversity of beetles. The herein phylogenetic study based on morphology of the Curculionoidea is considered much improved over past and more recent studies. While previous studies have included taxon samplings of no greater than ~150 terminal taxa, this study has incorporated a sampling of nearly four times those quantities. It provides revised cladistic-based hypotheses for several of the basal lineages and the first hypotheses for a few others (i.e., Anthribidae, Caridae). Within Curculionidae, a clade either beginning with Raymondionyminae or just after Dryophthorinae + (Scolytinae + Platypodinae) depending on which characters are chosen to define the groups, several hypotheses at the subfamilial level are revised as well as proposed for the first time. While several studies have attempted cladistic analyses of the superfamily, taxon sampling within Curculionidae has always been sparse, obstructing any desire for obtaining meaningful results pertaining to delimitation of the many diverse subfamilies classified within.

Aside from inadequacies in taxon sampling, past morphological studies have been fairly wanting in other ways. Indeed, while much has been accomplished with weevil morphology, particularly in studies which have examined ganglion structure, testes and ovary form, much has been left unexamined. Specific areas which have been overlooked, but which contain complex structural features and are integral to morphological study, include the internal structures of the rostrum, meso- and metathorax, including meso- and metanota, and hindwing axillary sclerites.

Many new characters also have been found in other regions of the body. One example is an unobserved ventral pair of aedeagal struts in the male terminalia of primitive members of Dryophthorinae, a feature considered transitional to Curculionidae, resulting in the postulation of non-homology of the aedeagal struts between members of Curculionidae and those lineages before Curculionidae. The importance of more detailed morphological observations is benefitial not only in providing increased resolution in the extant classification, but also in compiling a larger and more useful suite of features from which to identify fossil taxa. For example, the erection and subsequent expansion of the anomalous group Eccoptarthridae mostly was due to superficial character examination and failure to associate the extant fauna with fossil forms. Even a large portion of the diverse assemblage found at Karatau has been attributed to Nemonychidae due to cursory examinations and reliance on limited sets of morphological features. The studies herein, in attempts to remedy such inadequacies in morphology and fossil interpretation, have included morphological examinations of sclerotized anatomical features of the entire body (with the exception of soft tissue) and re-examinations of fossil type material from around the world. Incorporating such a vast sampling of fossil taxa also allows for the depiction of a much improved hypothesis of weevil diversification from at least the Late (probably Middle) Jurassic of the Mesozoic and continuing into the Tertiary.

Possibly one of the more interesting results from this phylogenetic study pertains to the position of the bark and ambrosia beetles, Scolytidae and Platypodidae. Previous studies examining weevil phylogeny, as well as specifically focusing on the above two lineages, have obtained a broad range of relationships in which Scolytidae and Platypodidae are monophyletic to polyphyletic and may be considered separate families to nested deep within Curculionidae. The results obtained herein places them within a single clade that is sister to Dryophthorinae.

While a few studies, mostly based on molecular data, have obtained a relationship of Platypodidae + Dryophthorinae, the scolytids typically have been hypothesized to be nested within Curculionidae in these studies. The bountiful morphological data and relatively large number of taxa studied here reveal several plesiomorphic features that are retained in scolytids and platypodids. While some of these features appear more related to or derived from Nemonychidae and Anthribidae, some also show striking similarity to Dryophthorinae. While this relationship may still be considered tentative, a much greater diversity of morphological data is now available for these groups, allowing for more robust hypotheses to be formed that at least demonstrate a more basal (not highly derived in Curculionidae) position of Scolytidae and Platypodidae.

While the studies herein do not contribute to past studies based on molecular datasets, they also have suffered from inadequate taxon sampling and several other suboptimal features. For instance, mitochondrial genes, including whole mitochondrial genomes, have been relied upon to recover Mesozoic-age divergences. Ribosomal secondary structure has not been referenced for sequence alignments of ribosomal genes, potentially leading to large problems in misalignment. Furthermore, although measures of clade support, such as bootstrap values, are indicative of the robustness of a certain topology given the dataset from which it was derived, in weevil phylogenetics it has been interpreted as the validity of the evolutionary relationships. Such results are problematic when little else is referenced beyond such support values to assess clade composition and the characteristics which may define such relationships. For the above reasons, a majority of the molecular studies conducted thus far concerning weevil phylogeny should be considered somewhat superficial. Indeed they have contributed to our understanding of weevil relationships, each in its own way, though the almost arbitrary relationships that have been obtained in the higher Curculionidae are somewhat disturbing and should be interpreted with caution.

From the studies, herein, including the comprehensive studies on rostrum tissue development and adult structure, a relatively robust framework has been established for incorporating developmental methods into ongoing studies of weevil evolution and initial insight gained towards understanding the formation of a peculiar key innovation, the weevil rostrum. As a result of the developmental study incorporating RNAi experiments, it is at least evident that BR-C plays a critical role in rostrum formation. Several isoforms may be involved in this patterning regime, including a putative new z6 isoform, and the interaction of these may operate through initial ecdysone signaling to initiate further downstream pathways, such as the EGFR pathway, which give rise to a distinct rostrum. Once a rostrum is produced, it also is apparent that hox genes and other transcription factors play roles in rostrum differentiation throughout the various weevil lineages, allowing for various modifications of the rostrum ranging from orientation, sclerite development, and ornamentation. Due to results indicating differential expression of *Armadillo* and *Pangolin*, PCP appears to be involved in directing the orientation of rostrum growth, giving rise to the observed variation in prognathous to opisthognathous rostrum orientations throughout weevils.

Future directions will largely focus on elucidating rostrum development, determining the major intersecting pathways involved in rostrum formation and differentiation, and comparatively applying such information in a phylogenetic framework. As evidenced by the external and internal changes in rostrum morphology, several possible key genetic changes have occurred in producing a few major rostrum forms and allowing for several events of rostrum shortening and elongation. Obtaining a more thorough picture of differences in transcript expression throughout the duration of rostrum tissue differentiation and proliferation also is of great desire. To do so, transcriptomes of several stages in *Sitophilus oryzae* will be obtained, beginning in the late 4$^{th}$ instar larva and continuing throughout the prepupa. Such information will provide a more detailed time-dependent portrayal of gene expression and may likely yield a greater number of candidate genes for further exploration in *S. oryzae* and the other model weevil taxa. Furthermore, certainly as other beetles and insects have evolved similar types of rostra (e.g., Mecoptera; Coleoptera: Lycidae, Salpingidae, Staphylinidae), examination in such taxa and comparison of the genetic elements involved in rostrum formation will provide insight into the evolutionary developmental mechanisms responsible for morphological convergence and possibly into mechanisms involved in mimicry.